CONTRIBUTION OF LIFE HISTORY CHARACTERISTICS TO LARVAL SETTLEMENT AND CONNECTIVITY OF *ACANTHURUS TRIOSTEGUS* IN WINDWARD O'AHU

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ABSTRACT

Life history characteristics of larval fish may contribute to determining how likely they are to settle at the end of their pelagic existence. However, there is a general lack of knowledge on the contribution of these characteristics to settlement success in specific species. This research investigates the contribution of life history characteristics, specifically pelagic larval duration (PLD) and ontogenetic vertical migration (OVM) to settlement success of larval *Acanthurus triostegus* in windward O'ahu coastal waters and Kāne'ohe Bay. This is done through model simulations using the Connectivity Modeling System (CMS), which is a particle dispersal model with ocean current velocities supplied from the Regional Ocean Modeling System (ROMS). The simulations are compared and analysed using generalized linear models in R statistical software. The main findings of this study are that larval settlement success is specific to regions of larval release and that the effect of life history characteristics, specifically variations in PLD and OVM behaviour on larval settlement success, are region of release specific as well. Overall, settlement success was highest for larvae released within Kāne'ohe Bay. Additional biological factors such as larval orientation and swimming behaviour could be added to expand this study in the future.

TABLE OF CONTENTS

List of Tables

List of Figures

INTRODUCTION

Coral reefs have great ecological, social, cultural and economic importance to Hawai'i. Coral reefs attract thousands of tourists, who enjoy snorkelling and appreciate the biodiversity on the reefs. Fishing at the reef is a common recreational activity during weekends and school holidays for many local families (Delaney et al. 2017). Fishing at the reef with the intention of taking home catch for a meal and to share among family and friends, also called subsistence fishing, is common in Hawai'i as well (Delaney et al. 2017). Subsistence fishing has been practiced in the Hawaiian Islands and other islands in Polynesia over generations, and is an important cultural and social activity (Grafeld et al. 2017, Delaney et al. 2017, McCoy et al. 2018). A study done by McCoy et al. (2018) for the period 2004 to 2013 revealed that an estimated 1,167,758 ± 43,059 kg of fish and invertebrates were caught each year from non-commercial reef associated fishing activities which included recreational, subsistence and cultural harvest in the Hawaiian islands. This was 84 percent of the total catch for the study period. The other 16 percent of the catch (184,911 kg of reef fish and invertebrates per year) was attributed to commercial activities (McCoy et al. 2018). Due to the high extraction rate of reef associated fish, proper ecosystem management strategies are fundamental to ensure reef fish populations are able to replenish themselves and continue to provide important ecological, social and ecosystem benefits.

Most reef fish have a pelagic larval phase. Knowing this and assuming that larvae passively drift in the open ocean with the currents during this phase, has made it easier for ecologists to simulate larval transport using coupled biological-physical particle tracking models (Paris & Cowen 2004, Paris et al. 2013, Faillettaz et al. 2018). They use ocean current velocities calculated from primitive equation models (for example the Regional Ocean Modeling System (ROMS)) to move virtual larvae in a specific region. The tracking models have been used to study the transport of larvae spatially and temporally, which is useful to inform decisions regarding the management of a target species within an area (Faillettaz et al. 2018). However, many times such models include very little information regarding the life history characteristics of a target species due to the lack of direct behavioural observations for specific species (Paris & Cowen 2004). Several studies have shown that life history characteristics of larval fish may have important consequences for their dispersal and are critical to explaining observations of their dispersal and connectivity; therefore it is important to include them in modeling studies (Paris & Cowen 2004, Treml et al. 2015).

An example of a larval life history characteristic is the length of the larval pelagic phase, also called the pelagic larval duration (PLD). The length of the pelagic phase of larval reef fish can vary from a few days to several months depending on which family the species belongs to. Damsel fish (Family Pomacentridae) for example may have a PLD of 10 to 15 days while surgeon fish (Family Acanthuridae) may have a PLD of 50 to 80 days (Randall 1961, Wellington & Victor 1989). Modeling studies comparing PLD among reef fish larvae have shown that species with shorter PLDs have shorter dispersal distances and higher self-recruitment, while species with longer PLDs have longer dispersal distances, wider distribution potential and stronger connections among reefs located further away from their natal reefs (Faillettaz et al.2018). While there have been several studies (e.g., Mayorga-Adame et al. 2017, Sanvicente-Añorve et al. 2018, Faillettaz et al.2018) that have looked at the effect of PLD on larval dispersal and population connectivity between different species, there have not been many studies looking at the effect of variation in PLD within a species on its larval dispersal and population connectivity. Variation in PLD within a species may arise from factors such as differences in growth and development rates between individuals due to being exposed to different water temperatures during development and/or due to differences in food availability (Dekshenieks et al. 1993, McLeod et al. 2013). McLeod et al. (2013), in laboratory experiments looking at growth, development and settlement in larval anemone fish, found that development and time to reach metamorphosis from larvae to juvenile was fastest in larvae in warmer temperatures (temperature within species tolerance level) with high food availability. Cooler water temperatures and low food availability resulted in slower development rates and longer time to reach metamorphosis and settlement (McLeod et al. 2013). In the natural environment larvae may be exposed to seasonal changes in water temperature and food availability, which may cause variations in their PLD. This variation in PLD within a species may influence their dispersal and connectivity patterns. It is important to include these variations in PLD in studies of larval dispersal and connectivity to get a full range of understanding of their dispersal and connectivity patterns.

Another example of a larval life history characteristic is ontogenetic vertical migration (OVM) behaviour. When spawning occurs in most reef fish, pelagic eggs are released (Randall 1961). Upon hatching, fats and lipids in the yolk sac keep the larvae buoyant (Randall 1961). As the fats and lipids are used up, the larvae begin to sink and develop vertical swimming behaviour to maintain their depth (Randall 1961). As the larvae grow and develop, they move deeper (Randall 1961). Once the larvae are competent to settle, they move back to shallow water

depths to settle in coastal settlement habitats (Randall 1961). This migration of larval fish to different depths with age is termed as ontogenetic vertical migration. This active depth seeking behaviour with age has been confirmed by Multiple Opening-Closing Net and Environmental Sampling System (MOCNESS) tows for several families of larval reef fish including Acanthuridae, Apogonidae, Serranidae and Pomacentridae in Tetiaroa (French Polynesia) (Irisson et al. 2010). In these MOCNESS tows, the centers of mass of larval patches were found deeper for the more developed larval stages (Irisson et al. 2010). Irisson et al. (2010) also found that the downward movement of the center of mass of a larval patch may occur over a range of depths with time and different families potentially occupy different depths. Several reasons have been identified to explain this downward vertical migration behaviour in larval fish, for example, as larvae grow and develop better visual systems, they may migrate to a depth where the light intensity is high enough to feed but low enough to avoid visual predators (Job & Bellwood 2000). Paris & Cowen (2004) suggest that OVM behaviour in larval fish may also act as a retention mechanism for local populations. Vertical migration may allow larvae to take advantage of the vertical shear in the water column and position themselves in shoreward moving currents which would increase their chances of reaching coastal settlement habitats (Paris & Cowen 2004, Irisson et al. 2010). Modeling studies of bicolor damselfish (*Stegastes partitus*) in Barbados show that the inclusion of OVM behaviour reduced advective losses of larvae with age and increased retention in the model (Paris & Cowen 2004, Paris et al. 2009).

In this study, I explore the contribution of life history characteristics, specifically the pelagic larval duration (PLD) and the ontogenetic vertical migration (OVM), to the settlement success of modeled *Acanthurus triostegus* larvae along the windward coast (north-eastern side) of the island of O'ahu in the Hawaiian Islands (Figure 1). This will help answer questions on whether including details of life history characteristics such as variations in PLD within a target species or active depth selection with age (OVM behaviour) in a particle tracking model has an impact on larval dispersal, settlement and connectivity patterns as opposed to larvae being modeled as passively drifting particles and with just one value for their PLD. This study will help quantify the contribution of life history characteristics to larval settlement success in a model. It will help determine if it is important to include life history characteristics such as variations in PLD or OVM in future modeling studies.

Acanthurus triostegus was chosen for this study because it is a commercially and socially important reef fish in the Hawaiian Islands (Smith 1993, Longenecker et al. 2008, Schemmel &

Friedlander 2017). In the olden days, Hawaiians collected post settlement forms of *A. triostegus* on reef flats by the basketful, which were later salted, dried and stored for trade or for subsistence use (Longenecker et al. 2008). Nowadays, most people enjoy the adult forms of *A. triostegus,* which can be prepared in a number of ways including pan-frying, grilling and baking (Temple 2013). The adult form can be caught using handlines, spear, traps and nets and has been ranked second among speared fish in Waikiki creel surveys in 2003 (Smith 1993, Longenecker et al. 2008). *A. triostegus* has been extensively studied in its natural environment and in laboratory settings in terms of its life history (Randall 1961; Longenecker et al. 2008), spawning behavior and life cycle (Robertson 1983), juvenile behavior (Sale 1968), reproductive characteristics (Walsh 1987, Schemmel & Friedlander 2017), impact of ocean currents on spawning and larval entrapment (Lobel 1989), geographic structure and gene flow (Planes 1994), and the effect of current and wind forcing on its population connectivity (Jerolmon 2016) in Hawai'i and in other areas in the Indo Pacific region. The information on direct behavioural observations of *A. triostegus* present in these studies made it easier to parameterize its life history characteristics in the biological-physical model used in the present study.

Another reason to investigate the contribution of life history characteristics to the settlement success of modeled *Acanthurus triostegus* larvae along the windward coast of O'ahu was that previous modeling studies by Jerolmon (2016) for the 2014 and 2015 study period suggested that biological factors may play a key role in explaining larval settlement success along the coastline, as physical factors such as winds and current patterns could not explain the differences in recruitment numbers observed between the two years. The summer of 2014 experienced a very large recruitment event (coined as "biblical" by the media), several families of larval fish were seen in high abundance on reefs around the Hawaiian Islands. The summer of 2015 however, had an abnormally low recruitment, perhaps a quarter or less than that what had occurred in 2014 (Talbot 2014, Jerolmon 2016). For this research, the *A. triostegus* spawning seasons for 2014 and 2015 were chosen as the study period as well. While the purpose of this research is not to fully explain the large recruitment event observed in 2014, with the life history characteristics explored in this study and the modeled ocean current velocities for 2014 and 2015, I hope to get an idea of how larval life history characteristics may have influenced settlement success of reef fish larvae during this period.

The windward coast of the island of O'ahu was chosen as the study site for this research because *A. triostegus* is naturally found on the reefs along this coastline. They can be seen grazing for algae on rocky areas devoid of coral cover during the day (Randall 1961). Another major reason for choosing the windward coast as the study site is because this study is intended to extend a previous study by Jerolmon (2016) which explored the relationship of larval settlement and connectivity patterns to physical factors such as winds, sea surface height gradients and current patterns in the same location by using a coupled biological physical oceanographic model. The physical oceanographic model used in this study and that used by Jerolmon (2016) was developed from the ROMS model configured by Conor Jerolmon and Professor Brian Powell in the Department of Oceanography at the University of Hawai'i at Mānoa. The model showed that there was strong current flow at the surface in the along shore direction (Figure 2 a, b), which was noted by Jerolmon (2016) as a possible cause for a lot of virtual larvae exiting the model grid in the along shore direction. Due to the presence of strong advection (in the along shore direction) near the surface and weak flows at depth, this coastline was an ideal place to test the effect of larval OVM behaviour (active depth seeking behaviour) on the retention, dispersal, settlement and connectivity patterns of virtual *A. triostegus* larvae in the model.

Although this study will simulate life history characteristics of *A. triostegus*, the results from this study can be used to infer dispersal patterns in other species belonging to Family Acanthuridae such as other surgeon fish, tangs and unicorn fish, which may be of interest from a fisheries or ecosystem management perspective due to these species having high economic value and/or high fishing pressure. Most members within Family Acanthuridae have similar life history characteristics.

This study will test three hypothesis, first, that ***PLD within a species may influence larval settlement success, with shorter PLD resulting in greater self-recruitment and longer PLD resulting in dispersal over greater distances, greater advection out of the study area and less self-recruitment.*** The second hypothesis is that, ***if the virtual larvae are able to move to 50m depth where advection is low, far from the surface where advection is high, then larval retention in the model area will be increased.*** Being retained in the model for a longer period of time may increase chances of virtual larvae settling in coastal habitats at the end of their pelagic phase. The third hypothesis is that the ***life history characteristics explored in this study along with the modeled ocean current velocities for 2014 and 2015 may help explain the high recruitment observed in the summer of 2014 in the Hawaiian Islands.***

This study explored potential biological and physical interactions affecting *A. triostegus* settlement variability via a coupled biological-physical model. The model combined a Lagrangian particle dispersal model, modeled high-resolution ocean current velocities and larval behaviour and life history characteristics specific to *A. triostegus*. Modeled settlement and connectivity estimates were then analysed statistically to determine which biophysical predictors explained the modeled settlement and connectivity patterns in *A. triostegus* in both space and time (e.g., 2014 and 2015)

METHODOLOGY

Study Area

The north-eastern side of the island of O'ahu in the Hawaiian Islands was chosen for the study site for this research (Figure 1). The north-eastern side of O'ahu receives the predominant northeast trade winds and is commonly called "windward O'ahu" (Ostrander 2008, Jerolmon 2016).

The windward O'ahu coastline is fringed by coral reefs extending 1-2 km from the shore, beyond which they gently slope to a depth of 12-13 m (Lowe et al. 2009, Figure 3). Juvenile and adult *A. triostegus* are commonly seen grazing around the reefs during day time. The reefs serve as habitat for *A. triostegus*; these are the locations adult fish release their eggs and their juveniles settle during recruitment events (Randall 1961). Areas on the reef devoid of coral but with rocky hard bottom substrate are ideal for the growth of fine filamentous algae on which juvenile and adult *A. triostegus* feed (Randall 1961). A fringing/barrier reef (average depth 3-5 m) also extends across the mouth of Kāneʻohe bay, a semi-enclosed estuarine-bay system on the windward coast of Oʻahu (Lowe et al.2009). Kāneʻohe bay is the largest sheltered body of water in the Hawaiian Islands with an along shore length of approximately 13 km and cross shore width of approximately 4 km (Lowe et al. 2009). The lagoon area within Kāneʻohe bay (1-2 km wide) has a depth of approximately 10-15 m and contains numerous patch reefs (Lowe et al. 2009). These patch reefs also serve as habitats for *A. triostegus* (Jerolmon 2016). Two main channels facilitate the exchange of water between Kāneʻohe bay and the ocean, a shipping channel (depth of approximately 15 m) in the north of the bay and the Sampan Channel (depth of approximately 5 m) in the southern part of the bay (Lowe et al. 2009). The southern inner-most part of Kāneʻohe bay is a semi-enclosed region that functions almost as a "bay within a bay" due to its geographic isolation, only connecting to the coastal ocean through two narrow channels on either side of an island called Coconut Island (Ostrander 2008, Lowe et al. 2009).

Oceanographic Model

Nested ocean current velocity fields were used in this study to simulate larval transport in the study area. The current velocities were generated by Professor Brian Powell in the Department of Oceanography at the University of Hawai'i at Mānoa using the Regional Ocean Modeling System (ROMS) output for the years 2014 and 2015. ROMS is a free-surface, terrain

following, primitive equations ocean model on an Arakawa C grid (Shchepetkin & McWilliams 2005).

A low resolution windward coast of O'ahu model and high resolution model for Kāneʻohe bay were created. The high resolution Kāneʻohe bay model was nested in the low resolution windward coast of O'ahu model (Figure 4). This was done to allow for finer scale calculations of the transport processes that occur in a bay to accurately simulate near-shore dynamics and coastal larval transport (Jerolmon 2016).

For the windward coast of Oʻahu, the ROMS output had a 1 km resolution grid with 20 vertical levels (s-levels) of ocean current velocities (Figure 4). The output of this model was saved as a snapshot every 3 hours. Open ocean boundary conditions for the windward coast model were obtained from the 4 km Hawaiian Islands ROMS model (Matthews et al. 2012). The 4 km Hawaiian Islands ROMS model also provided the tidal forcing for this model. Atmospheric forcing was provided by the Weather Research and Forecasting Model (WRF) (Michalakes et al. 2001). Bottom topography was supplied by the Hawaii Mapping Research Group (HMRG) of the Hawai'i Institute of Geophysics and Planetology at University of Hawai'i (Mānoa).

For Kāneʻohe bay, the ROMS output had a 100 m resolution grid with 20 vertical levels (s-levels) of ocean current velocities (Figure 4). The output of this model was saved as a snapshot every 30 minutes. The windward coast model was used to supply boundary conditions and the tidal forcing for the Kāneʻohe bay model. Atmospheric forcing was provided by the Weather Research and Forecasting Model (WRF) (Michalakes et al. 2001). Stream input was provided for Heʻeia, Waiheʻe, Waiāhole, and Waikāne Streams from the U.S. Geological Survey stream gage data (USGS 2016).Topography was created from the 4 m gridded bathymetry of Kāneʻohe bay made available through NOAA, with minor smoothing applied to average the data onto the 100 m grid spacing (after Jerolmon 2016).

As the particle tracking model used in this study required fixed depth levels, the windward coast and Kāneʻohe bay model outputs were re-gridded to have 41 fixed depth levels using an objective analysis with weighted decorrelation scales (Jerolmon 2016, B. Powell, personal communication, 2019). The 41 vertical levels were at 0.5-m intervals from the surface to 10 m, at 1-m intervals from 10 m to 20 m, at 25 m, every 10 m from 30 m to 50 m and every 25 m from 50 m to 200 m.

Next, these models were interpolated to an Arakawa A grid from the original Arakawa C grid used in ROMS, making the values of all variables available at the centre of each grid cell.

Moreover, a coordinate remapping was performed on the windward coast and the Kāneʻohe bay models as the particle tracking model used in this study required one dimensional longitude and latitude arrays. The x and y position of each point on each grid was first converted to a distance from an origin (the lower left corner of the windward coast grid) and then scaled to equivalent longitude and latitude about the equator.

Lastly, the 3 hr. windward coast model was linearly interpolated to 30 min. intervals to match the temporal resolution of the Kāneʻohe bay model. See Jerolmon (2016) for further details and model validation.

Particle Tracking Model

The Connectivity Modeling System (CMS) developed by Paris et al. (2013) was used as the particle-tracking model in this study. CMS is a Lagrangian particle-tracking model that employs a 4^{th} order Runge-Kutta scheme to transport virtual particles through a set of velocity fields from an oceanographic model (e.g., ROMS) with the ability to incorporate biological parameterization using an individual-based model (IBM) (Paris et al. 2013). CMS was used to simulate life history characteristics of *A. triostegus*. CMS was parameterized to provide virtual *A. triostegus* larval spawning times and dates, locations where the eggs would be released, behavioural characteristics (variation in PLD and OVM), oceanographic current velocities to move the larvae, vertical and horizontal turbulent velocity to add randomness to larval trajectories, and habitats to settle in once larvae reach competency (an age able to settle). CMS was chosen for this study because of its ability to work with nested grids (high resolution Kāneʻohe bay grid with lower resolution windward Oʼahu grid) and for the biological parameterizations available within CMS (Jerolmon 2016).

Habitat Polygons and Release Locations

Habitat areas across the windward coastline representing *A. triostegus* egg release and larval settlement locations were identified and defined as habitat polygons by a team of ecologists from the University of Hawaiʻi (Mānoa) (M. Donahue, personal communication, 2018) based on benthic habitat maps created by NOAA's National Centers for Coastal Ocean Science (NCCOS) (Figure 3). The ecologists were interested in areas with hard substrate types such as reefs and patch reefs which would serve as potential habitat for *A. triostegus*, and where filamentous algae, which are food for this species, could grow. Polygons were then drawn over

individual patch reefs and other potential habitat areas (Figure 5, Jerolmon 2016). Fifty three such habitat polygons were drawn across the study area (Figure 6 a, b). At the centroid of each habitat polygon was the egg release location (Paris et al. 2013, Jerolmon 2016). If the centroid of a polygon was on land, then the release location was redefined to be in the water. Release depth was set to 3 m for most locations, based on field observations of *A. triostegus* spawning aggregations (Sale 1968, Jerolmon 2016). If the model depth at the release location was less than 3 m, then the release point was set to half the depth at that location.

The 53 **habitat polygons** were then grouped into **regions** within the study area based on similar circulation patterns (Bathen 1968, Lowe et al. 2009). These regions are North Coast (polygons 1-8), Mid Coast (polygons 9-16), North Bay (polygons 17-18), Mid Bay (polygons 19-26), South Bay (polygons 27-29, 31, 44), Inner Bay (polygons 30, 32-36), Reef flat (polygons 37-43), Mokapu (polygons 45-47) and South Coast (polygons 48-53) (Figure 6 a, b).

The Seascape Module in CMS was used to create habitat polygons in the model simulations, which functioned as release and settlement locations for the virtual *A. triostegus* eggs and larvae.

Simulations and Biological Parameterization

A total of 176 simulations were performed, grouped into 8 sets. These included 1 set of 32 simulations where larvae were used as drifters, passively advecting in the currents without diffusion, 3 sets of simulations exploring pelagic larval duration (PLD) (96 simulations) and 4 sets of simulations exploring ontogenetic vertical migration (OVM) (48 simulations) (Table 1). The virtual egg release dates for the simulations were obtained from the 2014 and 2015 *A. triostegus* spawning seasons in Hawai'i, which lasts from December to July (Randall 1961, Schemmel & Friedlander 2017). As spawning in this species has been observed to occur during afternoon ebb tides around full and new moons, the dates of full and new moons each month from December to July for 2014 and 2015 were chosen as the virtual egg release dates for the simulations (Randall 1961, Lobel 1989, Schemmel & Friedlander 2017). A total of 32 egg release dates were used (see Table 1). Egg release times were set to 03:00 UTC (Hawaii Standard Time (HST) + 10) to simulate afternoon (5pm) ebb tides in Hawai'i. The 2014 and 2015 spawning seasons were chosen for this study to help explain the large recruitment event observed in the summer of 2014 in the Hawaiian Islands (see Introduction).

The timing of the pelagic larval duration and settlement window were chosen based on *A. triostegus* PLD estimates of 54-72 days (Randall 1961, Longnecker & Langston 2008) and settlement window of 10 days, from the collection of recruiting juveniles from tide pools in O'ahu by Randall (1961). Most simulations ran for 65 days; larvae within any habitat polygon during the last 10 days were considered to have settled. In the simulations where PLD variation was tested, the settlement windows were shifted to 65-75 and 75-85 days.

Virtual larvae advected to an open ocean boundary (outlined in red in Figure 4) were considered lost from the simulation. The 'avoidcoast' flag in CMS was set to prevent particles from becoming stranded on land. (Surprisingly, however, in some of the simulations particles became stranded in the shallow areas within Kāneʻohe Bay). The 'upper level surface' flag in CMS was likewise set to prevent larvae from passing through the sea surface. The turbulence module in CMS was employed to perturb each larva in a random direction to simulate larval motion on scales smaller than the grid resolution (Paris et al. 2013). A random velocity vector with a bivariate normal distribution for U and V, and a normal distribution for W, was added to the ocean velocity, herein referred to as turbulent velocity (Jerolmon 2016). Horizontal and vertical diffusivities were used to calculate the random velocity vector (Paris et al. 2013). The horizontal diffusivity used for the Kāneʻohe Bay grid was 0.2 m^2/s, after Lowe et al. (2009). For the windward coast grid, a value of 2 m^2/s was used to account for the lower (by a factor of 10) resolution of the grid (Jerolmon 2016). A value of 0.001 m^2/s (per grid) was used for vertical diffusivity for both the grids as CMS required a single value for vertical diffusivity, rather than depth varying profile (Jerolmon 2016). The vertical diffusivity value represented the average vertical diffusivity in a turbulence model comparison study by Durski et al. (2004). The turbulence time step was set equal to the CMS model time step at 300 s, so that the random effect given by the turbulent velocity was applied at each time step.

Currents: advection without diffusion

Simulations were designed to understand the influence of ocean circulation patterns on larval trajectories in Kāneʻohe bay and windward O'ahu. No turbulent velocity (random movement) was added to the virtual larvae in these simulations, the larvae were used as neutrally buoyant, passive drifters. In this set of simulations only 1 egg was released from each habitat polygon per egg release date (Table 1). The eggs passively drifted in the ocean currents until they

reached competency at 65 days and were allowed to settle in the model. All 32 egg release dates were used.

Pelagic Larval Duration (PLD) Simulations

The effect of varying PLD on settlement success of *A. triostegus* was explored. Three levels of PLD were used: 55 days, 65 days and 75 days. Three sets of simulations were conducted, 1 set for each level of PLD used (Table 1). Each set of simulations was run for the 32 egg release dates. On each egg release date 100 eggs were released in each of the 53 habitat polygons. One hundred was chosen as the number of eggs to be released from each habitat polygon per egg release date although 22,000 to 362,000 pelagic eggs per female are released in nature per spawning event (Longenecker et al. 2008) because of computational limitations. Larvae were set to be neutrally buoyant with additional turbulent velocity applied, which provide randomness to larval trajectories (turbulent velocity described in Simulations subheading). Depth of release was set to be 3 m. The settlement window was set to be 10 days. The total length of each set of simulations was 65 days, 75 days and 85 days respectively.

Ontogenetic Vertical Migration (OVM) Simulations

The effect of Ontogenetic Vertical Migration (OVM) life history characteristic on settlement success was explored in 4 sets of simulations. Only 12 of the 32 egg release dates were used in each set due to computational limitations. The 12 egg release dates were chosen to equally represent egg release dates in the winter, spring and summer months. As spawning occurs twice each month, at full and new moons, 2 egg release dates (full and new moon dates) were chosen for each month representing winter, spring and summer. The winter egg release dates for the 2014 and 2015 spawning seasons were chosen from January, the spring egg release dates were chosen from March and the summer egg release dates were chosen from June (Table 1).

Each of the 4 sets of simulations used to explore OVM used a different approach to modelling larval transport in the vertical. In the first set of simulations no OVM behaviour was added to the larvae; once the egg was released, it was set to be neutrally buoyant with turbulent velocity added at every time step. This simulation can be considered as the control as no OVM behaviour was used. In the second set of simulations *A. triostegus* OVM behaviour was

simulated by using the Vertical Migration Module from the Individual Based Model (IBM) component of CMS. Through the Vertical Migration Module, the virtual *A. triostegus* larvae were made to be neutrally buoyant (with turbulent velocity added in the horizontal) for the first 20 days after release at a depth of 3 m. This was because larvae were assumed to be lacking complex structures, which would enable them to actively move away from the depth at which they were released (3 m) (Randall 1961, Riis-Vestergaard 1984). For the next 20 days, larvae were moved to 50 m depth, the average depth that larvae may occupy in the pelagic (range 0-90 m) from MOCNESS tows by Irisson et al. (2010). For the last 25 days, the virtual larvae were made to move back to 3 m as larvae tend to move to shallow reef flats and tide pool areas towards the end of their pelagic larval duration to transform into juveniles (Randall 1961). If the target depth (3 m or 50 m) could not be obtained because of virtual larvae being in a shallow environment, their existing depth would be maintained and larvae would only be allowed to move horizontally not vertically.

In the third and fourth set of simulations the effect of having positively buoyant pelagic eggs in addition to OVM behaviour was explored. The only difference between the second set of simulations and the third and fourth sets was that there was no distinct egg phase in the second set. The exact value for the buoyancy of *A. triostegus* eggs is not known but a modeling study by Sundby and Kristiansen (2015) suggested that buoyancy for most pelagic eggs ranged from 0.001 to 0.002 g/cm^3. To explore the effect of having highly buoyant pelagic eggs (buoyancy = 0.002 g/cm^3) and less buoyant pelagic eggs (buoyancy = 0.001 g/cm^3) on larval dispersal and connectivity, the Mass Spawning Module and Buoyancy Module (IBM component of CMS) were employed. An egg diameter of 0.7 mm, the average diameter of ripe eggs from Randall (1961) was used. Egg density was calculated from the egg buoyancy 0.001 g/cm^3 in the third set of simulations for high density egg and 0.002 g/cm^3 in the fourth set of simulations for low density egg. The difference between water density and egg buoyancy was used to obtain egg density. Water density was obtained from the average density of water in the Kāneʻohe Bay grid at 3 m depth for the day of release as most particles that reach maturity are retained within the bay. The Stokes formula was used to calculate the velocity derived from egg buoyancy. This velocity was then added to vertical velocity from the oceanographic model with added turbulent velocity to move the egg in the vertical direction (Paris et al. 2013). Horizontal velocity from the oceanographic model with added turbulent velocity was used to move the eggs in the horizontal direction. An egg hatch time of 1 day was specified (Mass Spawning Module). For *A. triostegus* the egg hatches in 26 hours or 1.08 days (Randall 1961). As CMS

required an integer number of days for hatch time, 1 day was used. After the egg hatches, OVM behaviour starts and the virtual larvae follows the OVM behaviour specified in the vertical migration matrix.

After each simulation was completed in CMS, information on the trajectories of each larvae and where they settled were obtained. Other information such as the distribution of larvae with depth and time, whether larvae exited the model before the end of the simulation and what the cause of the exit was, were also obtained (Paris et al. 2013). The information on larval trajectories was used to make larval trajectory plots and stacked plots to understand what percent of larvae settled, what percent advected out of the model grid and what percent remained in motion, for each set of simulations, for each egg release date and each habitat polygon. For larvae that settled successfully, information such as larval release dates, settlement dates, the habitat polygons from which the larvae were released, and the habitat polygons in which larvae settled were used to show connectivity patterns. This information was also used to create inputs for statistical analysis using a generalized linear model (details in Statistical Analyses section).

Statistical Analyses

A generalized linear model (GLM) was used to quantify the effect of egg release date, region of egg release, biological parameters (pelagic larval duration (PLD) and ontogenetic vertical migration (OVM)) and their interactions with egg release date and region of egg release on *A. triostegus* settlement success along windward O'ahu. The predictor variables, egg release dates, region of egg release, PLD and OVM were set as categorical as the levels used in each predictor were assumed to be independent of each other. Here, the response variable, a boolean settlement result, was considered successful when larvae entered or were located within a habitat polygon during the competency period (the 10 day settlement window after the specified PLD had been reached). A generalized linear model allows expected values of response variables with non-normal distributions (binomial distribution in this research) to be related to a linear combination of predictor variables via a link function. While the response variable has a binomial distribution (a successful settlement would be a '1' and an unsuccessful settlement would be a '0'), the expected value is the probability of occurrence of a '1' or probability of a successful settlement. A logit link function was applied to the expected value

(probability of settling). This is the natural log of the odds ratio. This allowed interpretations to be made regarding the linear combination of predictor variables.

A generalized linear model was used to quantify the effect of varying PLD on the settlement success (Settled) of *A. triostegus* larvae, where PLD was a categorical variable with three options, 55 days, 65 days and 75 days, Release date was a categorical variable with 32 egg release dates (described in Simulations subheading) as options and Regions of release was a categorical variable with 9 regions (described in Habitat Polygons and Release Locations section) as options. Using the notation of R formulas, the model is summarized as:

Settled ~ PLD + Release date + Region of release + PLD:Release date + PLD:Region of release + Release date:Region of release (1)

where the interaction terms (denoted by ":") were used to allow the effects of PLD to vary by Release date and Region of release.

Another generalized linear model was used to quantify the effect of OVM on the settlement success (Settled) of *A. triostegus* larvae, where OVM was a categorical variable with four options: No OVM, OVM, OVM with low density egg and OVM with high density egg, Release date was a categorical variable with 12 egg release dates (described in Ontogenetic Vertical Migration (OVM) Simulations subheading) as options, and Regions of release was a categorical variable with 9 regions (described in Habitat Polygons and Release Locations section) as options. Using the notation of R formulas, the model is summarized as:

Settled ~ OVM + Release date + Region of release + OVM:Release date + OVM:Region of release + Release date:Region of release (2)

where the interaction terms (denoted by ":") were used to allow the effects of OVM to vary by Release date and Region of release.

The models were fit and model choices (linearity of relationships, error distribution assumption) were assessed (i.e. can the model give rise to the data?) by visually comparing simulated data to observations (via the DHARMa package in R; Hartig 2018). Model variants representing all possible combinations of these predictors (main effects and interactions) were

compared using the MuMin package (Barton 2018). Each combination was fit and the resulting model fits were compared according to the corrected Akaike Information Criteria (AICc) and the Bayesian Information Criterion (BIC). The best-specified model(s) were determined as those models within 2 of the lowest BIC or AICc value or Δ AICc / BIC ≤ 2. The AICc favors the predictive power of the model compared to BIC, while the BIC penalises more complicated models (models having more predictors) more heavily and selects the simpler model (Gove et al.2016, Wong-Ala et al. 2018). Using these criteria one model was selected to test the effect of PLD on larval dispersal, settlement and connectivity and one model was selected to test the effect of OVM on larval dispersal, settlement and connectivity (Table 1).

The influence of each predictor in the best-specified model was determined using hierarchical partitioning (hier.part package in R; Walsh & Mac Nally 2013). Hierarchical partitioning examines the effect of removing each predictor from models representing all possible combinations of predictors and gives the average independent contribution to explained deviance by each predictor (e.g. Gove et al. 2016). Modelled mean probability of settling by each predictor variable was calculated using the 'lsmeans' package in R (Lenth 2018). Pairwise comparisons between the different options in each predictor were made using Tukey's Method (lsmeans package in R; Lenth 2018). All data manipulation and statistical analyses were performed using R (R Core Team 2016 and related packages) unless otherwise specified.

RESULTS

This study explored the contribution of life history characteristics - specifically the pelagic larval duration (PLD) and the ontogenetic vertical migration (OVM) behaviour - on the dispersal, connectivity and settlement success of modeled *Acanthurus triostegus* larvae along the windward coast (north-eastern side) of the island of O'ahu in the Hawaiian Islands. The main question that this study aimed to answer was whether including details of larval life history characteristics such as variations in PLD within a target species and OVM behaviour (active depth selection with age) in a particle tracking model had an impact on modeled larval dispersal, settlement and connectivity patterns as opposed to larvae being modeled as passively drifting particles and with just one value for their PLD. Another important question that this research aimed to answer was how much influence each predictor (region of larval release, release date, PLD and OVM) had on predicted *A. triostegus* larval settlement success.

An analysis of larval trajectories and exit statuses revealed that approximately 32 % of all the larvae released in the simulations exploring variation in PLD settled at the end of their pelagic phase (please note that there is no mortality in this model), the other 68 % exited the model grid at the grid boundaries during the simulations (Figure 7). Larvae with shorter PLD had higher instances of settling, while larvae with longer PLD had higher instances of exiting the model grid at the grid boundaries (Figure 7). In the simulations using some form of OVM, approximately 20 % settled, approximately 70 % exited the model grid at the grid boundaries and approximately 10 % were stranded (Figure 8). For simulations where no OVM was used, approximately 32 % settled and 68 % exited the model grid at the grid boundaries. No larvae were stranded during these simulations. Larvae with no OVM had higher instances of settling, followed by larvae with some form of OVM (Figure 8). Simulations using only OVM had the highest instances of exiting the model grid at the grid boundaries, followed by OVM with high density egg and OVM with low density egg. This trend was opposite for the instances of larvae getting stranded (Figure 8). Simulations with no OVM had the lowest instances of larvae exiting the model grid at the grid boundaries (Figure 8).

The best specified statistical models exploring the effects of variation in OVM or PLD on settlement success are given in Table 2. Results from the generalized linear modeling indicate that region of larval release played the most important role in determining larval settlement success in windward O'ahu. Hierarchical partitioning in R revealed that region of larval release

explained the most variation in larval settlement success, pseudo r^2 = 0.404 (from the best specified model to explore PLD) and pseudo r^2 = 0.468 (from the best specified model to explore OVM). This was followed by release date with pseudo r^2 = 0.013 (from the best specified model to explore PLD) and pseudo r^2 = 0.028 (from the best specified model to explore OVM) and OVM with pseudo r^2 = 0.016. PLD explained the least amount of variation with pseudo r^2 = 0.001. Two-way interactions between OVM or PLD and release date and region of release were also included in the best specified model (discussed below).

Region of larval release

Modeled mean probability of settling or least-squares means from the best models employed to explore variation in PLD and OVM showed similar patterns of settlement success by region of larval release (Figure 9 a, b). Larvae released in regions within Kāneʻohe bay had higher settlement success than larvae released in other regions along windward Oʻahu (Table 3 a, b). Larvae released in Inner Bay region had the highest probability of settling (0.912 ± 0.001 from PLD simulations and 0.938 ± 0.002 from OVM simulations, Table 3 a, b). This was followed by larvae released in South Bay and Mid Bay regions (0.715 ± 0.002, 0.573 ± 0.002 respectively from PLD simulations and 0.718 ± 0.004, 0.288 ± 0.003 respectively from OVM simulations, Table 3 a, b). The probability of settling for larvae released in regions outside of Kāneʻohe bay were negligible in both the PLD and OVM simulations (Table 3 a, b). These results were supported by larval trajectories from the simulations. Larval trajectory diagrams indicate that most larvae released within Kāneʻohe bay tend to be retained within the bay and successfully settle by the end of the simulation (Figure 10 a). Kāneʻohe bay also acted as trap for larvae that kept those released outside of the bay from advecting out of the model grid, keeping them in the model longer and resulting in successful settlement at the end of the simulation (Figure 10 b). The high concentration of larval connections within regions in the bay revealed through larval connectivity patterns (Figure 11, for PLD and Figure 12, for OVM), indicate that there is high self-recruitment in Kāneʻohe bay. A general pattern of larvae moving from the central parts of the bay (Mid Bay and South Bay regions) to the more southern parts of the bay (Inner Bay regions) was also observed.

Release date

Release date was another important predictor explaining larval settlement success. Several potential seasonal patterns were identified from the simulations exploring variation in PLD (Figure 13). For example there was a peak in settlement success for larvae released around April 2014 and 2015 in the Mid Bay, Reef flat and North Bay regions. While the simulations only extended for two years, similar patterns in settlement success in 2014 and 2015 suggest that a seasonal trend may exist.

Ontogenetic Vertical Migration (OVM)

The best specified statistical model exploring the effect of variation in OVM behaviour found important effects of OVM and its interactions with region of release and release date on larval settlement success (Table 2). Different OVM types resulted in different levels of settlement success in different regions (Figure 14). For example for Inner Bay region, larval settlement success was highest when larvae only had OVM behaviour (no egg phase). For South Bay region, it was highest when larvae had OVM with high egg density. For Mid Bay, Reef flat and Mid Coast regions larval settlement success was highest when larvae had no OVM (Figure 14).

A striking effect of the use of OVM behaviour was that most settlements occurred in the Inner Bay region (Figure 12 b-d). Larval trajectories in simulations using OVM also showed that most larvae released within Kāneʻohe bay settled in Kāneʻohe bay (Figure 15). This indicated that many of the larvae that settled during the simulations using OVM may not have left Kāneʻohe bay at all and may not have participate in the intended OVM behaviour (i.e., moving from 3 m to 50 m and back to 3 m), as the depths inside Kāneʻohe bay are shallow (max depth is ~16 m). In CMS when the intended depth during vertical migration is not found due to larva being in shallow waters, its existing depth is maintained and the larva is only allowed to move in the horizontal. This suggests that the probabilities of settling expressed by the different OVM behaviours in this study may primarily be due to horizontal velocities rather than the intended OVM behaviour where active depth selection occurred with age. Histograms of depths occupied by larvae during simulations exploring OVM showed that a very small number of larvae engaged in the intended OVM behaviour and went to 50 m depth (Figure 16). As the depth of 50 m is only available in the open ocean outside Kāneʻohe bay where advection at the surface is high, many of the larvae that descended to 50 m depth were advected out of the model grid upon their vertical ascent (Figure 17). This exit occurred in two sets. The first set

(black to purple colors, Figure 17) indicates larvae that exit the model grid before engaging in ontogenetic vertical migration behaviour as their maximum age is up to 20 days. The other set (medium orange to yellow colors, Figure 17) indicates larvae that exit the model grid after engaging in ontogenetic vertical migration behaviour as they have ages between 40 to 55 days.

Pelagic Larval Duration (PLD)

The best specified statistical model exploring the effect of variation in PLD found important effects of PLD and its interactions with region of release and release date on larval settlement success (Table 2). While there was a general trend of larvae with shorter PLD having higher settlement success than larvae with longer PLD, this varied with region of larval release (Figure 18) and release date (Figure 19). Higher settlement success with shorter PLDs was most obvious in larvae released in the South Bay, Mid Bay, North Bay and Reef flat regions (Figure 18). Larvae released in Mid Coast and Inner Bay regions did not show large differences in settlement success between the different PLDs. Shorter PLD larvae also had higher settlement success than longer PLD larvae across most of the release dates (Figure 19). While the connectivity plots created for the three PLDs used were visually similar, the actual number of larvae settling the in simulations with shorter PLDs was higher than in simulations with longer PLDs (Figure 10 a-c). For example the number of larvae released from Inner Bay region that settled in Inner Bay region was 14,171 in the PLD 55 days simulation, 13,781 in the PLD 65 days simulation and 13,552 in the PLD 75 days simulation (Figure 11 a-c).

Current Patterns

Trajectory patterns in the simulations where larvae were used as passively advecting drifters (advection without diffusion, see Methodology section) show that current patterns influence larval settlement success as well. Large numbers of larvae exit the model grid (for example release date 2015-02-03 in Figure 20 a and release date 2015-06-02 in Figure 20 b, when there is increased flow in the along shore direction (Figure 21 a, b).

Furthermore, an investigation of larval trajectory plots in the PLD simulations suggest that episodic onshore currents early on in the simulations may have an influence on larval settlement success. For example, trajectories of larvae that successfully settled after being released in April 2015 from a polygon in the Reef flat region, one of the regions where highest

settlement success occurred in April show that larvae were generally being pushed deeper into the bay (Figure 22 a). Episodic onshore currents were observed within the day of release for the April 2015 release date (Figure 22 b).

Large recruitment event in Summer 2014

Although one of the aims of this research was to explain the large recruitment event that happened in Hawai'i in the summer of 2014 (see Introduction), model results from the predictors explored in this study (region of release, release date, PLD, OVM and their interactions) do not show significant differences between 2014 and 2015 that could account for the event.

DISCUSSION

This study investigated the contribution of life history characteristics - specifically the pelagic larval duration (PLD) and ontogenetic vertical migration (OVM) - on the settlement success of modeled *Acanthurus triostegus* larvae along the windward coast of O'ahu in the Hawaiian Islands. This study found that the most important predictor determining larval settlement success in the model was region of larval release. While other predictors; release date, PLD, and OVM and their interactions were important to explaining settlement success, their influence on larval settlement success was less than region of release.

The hypothesis that variation in PLD may influence larval settlement success (shorter PLD resulting in higher settlement success and higher self-recruitment vs. longer PLD resulting in lower settlement success, greater loss from the model grid, and lower self-recruitment) was consistent with results from releases in most regions in Kāneʻohe bay. These regions were; South Bay, Mid Bay, North Bay and Reef flat regions. While larvae released in Inner Bay region had the highest settlement success overall, Inner Bay region did not show a large difference in the probabilities of settling between the different PLDs used, hence the hypothesis is accepted for South Bay, Mid Bay, North Bay and Reef flat regions and rejected for the Inner Bay region. The hypothesis was not supported by the releases outside the bay due to negligible settlements occurring in larvae released in these regions. This suggests that for South Bay, Mid Bay, North Bay and Reef flat regions, when PLD is shorter, (for example during summer when waters are warm and larval growth and development occur at a higher rate), larvae released in these regions will have higher settlement success, while in winter when larval growth and development is slower and PLD is longer, larvae released in these regions will have lower settlement success. These results also suggest that at any moment regardless of seasons, species with shorter PLD released in South Bay, Mid Bay, North Bay and Reef flat regions will have higher settlement success than species with longer PLD released in the same regions.

The second hypothesis that was being tested in this study was that if virtual larvae are located deeper (at 50 m depth), then retention in the model area would be increased. While migration to 50 m depth did result in a longer residence time in the model for some of the larvae (Figure 17 a), many of the larvae that were in Kāneʻohe bay did not engage in this migration as a depth of 50 m was not available in the bay. Kāneʻohe bay had a maximum depth of 16 m. For many of the larvae in shallow areas such as within Kāneʻohe bay, the vertical migration module in

CMS, which gave larvae OVM behaviour, pinned the larvae close to the surface and restricted their movement to the horizontal direction. Most of these larvae that were trapped or retained within and around Kāneʻohe bay successfully settled at the end of the simulation, while most of the larvae that engaged in the specified OVM behaviour outside Kāneʻohe bay and migrated to 50 m depth got advected off of the model grid upon their vertical ascent due to high advection at the surface in the open ocean. If there was parameterization to allow larvae to have swimming and orientation toward the coast after vertical ascent, then it would have more accurately simulated larval OVM behaviour. In addition, some larvae were stranded in OVM simulations due to a model artefact in the way CMS handles vertical migration which underestimated the likelihood of settling for larvae released in some of the regions within Kāneʻohe bay (Figure 17 b). Had no larvae been stranded during the simulations using vertical migration, I believe that settlement success would have been different for each simulation type and the number of larvae exiting the model grid at the grid boundaries would have reflected this – this will be discussed in more detail later in the text.

Although model findings did not show differences in 2014 and 2015 that could account for the large recruitment event observed in the summer of 2014 in Hawai'i, some potential seasonal patterns in settlement success were identified between the two years. There was a peak in settlement success for larvae released in March and April 2014 and 2015 in the North Bay, Mid Bay and Reef flat regions. These patterns seemed to be related to currents however the responsible current patterns could not be readily identified (Figure 23 a, b). Larval trajectory diagrams for larvae released within the Reef flat region suggested that episodic onshore currents within the day of release may have an influence on larval settlement success (Figure 22 a, b). However, a comparison between the average cross-shore currents, where positive indicated currents moving off-shore and negative indicated currents moving onshore, found weak correlation (r-squared = 0.13) between onshore current flow and settlement numbers for larvae released in Reef flat region (Figure 24).

To explain the large recruitment event in the summer of 2014 (see Introduction), an investigation of larval dispersal corridors along windward O'ahu may be required. It is possible that shifts in larval dispersal corridors may have brought large numbers of larval fish to reefs in Hawai'i in the summer of 2014 (Karkarey &Theo 2016). Investigating larval dispersal corridors may be done with *in situ* video surveillance during recruitment events at different sites along a study area or by other efforts in documenting sizes of schools of recruiting juveniles at different locations along reefs in Hawai'i. It is also possible that warmer

temperatures locally around the Hawaiian Islands in the summer of 2014 could have resulted in fish larvae growing and developing faster, thus having a shorter PLD, resulting in large numbers of recruiting juveniles. Laboratory experiments in larval anemone fish have shown that a 1.5 ˚C difference in water temperatures can result in a 50 % difference in the time to reach metamorphosis (McLeod et al. 2013). As previously mentioned, in general greater number of larvae settle in simulations where larvae have shorter PLDs. Hence, with small increases in ocean temperatures, faster growth and development rates in larval reef fish may occur, causing PLDs to be shorter and increase chances of settling.

Results replicate findings from Jerolmon (2016) and Lowe et al. (2009) in that high settlement success and high self-recruitment was observed for regions in the south-eastern part of Kāneʻohe bay (Inner bay and South bay regions). This was likely due to sluggish circulation in these regions and limited exchange with other parts of Kāneʻohe bay and the coastal ocean. Lowe et al. (2009) found high particle retention (period 1-2 months) for Inner bay region when compared to the rest of Kāneʻohe bay (1-6 days). In addition, it was identified that along-shore currents led to loss of larvae across the model grid boundaries, which was also observed by Jerolmon (2016). The transport of larvae from the north or central regions of Kāneʻohe bay to southern regions of Kāneʻohe bay has also been validated through genetic studies. Genetic studies looking at parent offspring pairs around O'ahu located parents in northern parts of Kāneʻohe bay (North Bay region), which sent offspring to the southern parts of the bay (South Bay region) (R Coleman 2019, personal communication). Current circulation patterns in Kāneʻohe bay suggest that larvae may be advected into the South Bay and Inner Bay regions from the North Bay and Mid Bay regions during flood tides (Figure 25 a) and during sustained onshore current flow (Figure 25 b). This study also replicated findings from a modeling study done by Sanvicente-Añorve et al. (2018) in the Gulf of Mexico where shorter PLD larvae exhibited greater settlement success and less advection out of the model grid (shorter dispersal distances), while larvae with longer PLDs had lower settlement success and greater advection of larvae out of the model grid (longer dispersal distances). However, in the case of windward O'ahu and Kāneʻohe bay this trend was region specific. The trend of larvae with shorter PLD having higher settlement success was apparent in the South Bay, Mid Bay, North Bay and Reef flat regions.

As both empirical (genetic studies) and model outputs indicate that regions within Kāneʻohe bay may be self-seeding, it is important from an ecosystem management and fisheries management standpoint that these regions be monitored for local stressors such as pollutions

and over harvesting so that good ecosystem health is maintained and populations can replenish themselves.

The findings from this study can be applied to other fishes in Family Acanthuridae as most species within this family have similar life history characteristics, which may be important to fisheries managers interested in understanding population dynamics of the commercially important species and species with high extraction rates.

This study was limited in several ways. First, larvae reaching grid boundaries were permanently removed from the model domain, while in nature larvae may re-enter the study area during current reversals. This loss of larvae at the grid boundaries underestimates retention in the study area and total recruitment. Second, the study was limited in terms of the biological parameterizations available. Lack of parameterization for larval swimming and orientation behaviour in the vertical migration module in CMS resulted in competent larvae unable to locate the coastal habitat polygons and getting advected out of the model grid due to surface currents. Third, this study only considered larvae released at full moon and new moon while in nature some spawning may occur every day (but mostly within a few days around new moon and full moon) (Schemmel and Friedlander 2017). Exploring the influence of egg release dates around new moon and full moon on larval settlement success, dispersal and connectivity patterns could provide a better understanding of larval population dynamics and stronger seasonal patterns, - something for future studies to consider. Next, there were limitations due to the design of CMS. There is a need for the developers of CMS to review the way CMS uses the 'avoidcoast' flags (see Methods section, Simulations subheading) with the vertical migration module. Once the 'avoidcoast' flags are turned on, CMS should prevent larvae from becoming stranded on land or the sea floor, but simulations using the vertical migration module showed that some larvae got stranded even when the avoid coast flag was turned on. Moreover, there was a limitation due to the way in which the windward coast model was created. The model contained several model restarts and initialization periods, which caused chaotic velocities for up to 24 hours after each restart time. This limitation may have caused more larvae to exit the model grid if the restart times and chaotic velocities occurred a few days after larval release events. While having a continuous simulation would be best for studies of this sort, I was only able to have access to the present model.

Coupled biological-physical models are a useful tool to get an estimation of larval dispersal patterns and are critical for understanding larval connectivity but adequate parameterisation of

models is important. For example, for a simulation where the open ocean is involved, an IBM with parametrizations to allow larval orientation and swimming behaviour may be necessary for virtual larvae to locate coastal habitats. Future research could use IBMs that incorporate larval orientation and swimming behaviour once larvae reach competency to get a better understanding of larval OVM behaviour. Furthermore, future studies could compare model findings with data from ecological studies to validate the accuracy of modeling studies. This will require close monitoring of recruiting (newly settled) larvae at various habitat regions.

CONCLUSION

Modeling life history characteristics of larval fish, while important for ecological studies, is challenged by several factors: for example, the oceanographic models need to be configured correctly and the particle dispersal models need to be free of model artefacts. The benefits of using coupled biological-physical models, however, outweigh these challenges. Coupled biological-physical models are useful tools to estimate dispersal patterns of larval fish and to understand the contribution of certain biological predictors such as life history characteristics or physical predictors such as ocean currents to larval settlement success, dispersal and connectivity. This is important to better inform fisheries management decisions regarding particular fish species in particular regions.

This study used a coupled biological-physical model with CMS as the Langrangian particle dispersal model coupled to oceanographic current velocities calculated by the ROMS model. These coupled models were used to understand predictors (region of larval release, larval release dates and life history characteristics such as PLD and OVM) that influenced settlement success of *Acanthurus triostegus* larvae in windward O'ahu. Region of larval release had the greatest influence on settlement success, indicating that currents in specific regions play a large role in determining larval settlement success. Sluggish circulation patterns within Kāneʻohe bay contributed to greater self-recruitment within regions in Kāneʻohe bay, while greater advection in habitat regions outside of Kāneʻohe bay resulted in greater exit of larvae at the model grid boundaries. Larval release dates and life history characteristics, were important to explaining larval settlement success as well. A weak correlation was identified between onshore current flow and settlement numbers for larvae released in the Reef flat region.

Within the PLDs explored, a general trend of larvae with shorter PLD having higher settlement success and larvae with longer PLD having lower settlement success was observed at South Bay, Mid Bay, North Bay and Reef flat regions. The effect of PLD, however, was region specific.

Migration to 50 m depth during OVM did result in a longer residence time in the model for some of the larvae. However, lack of parameterisation for swimming and orientation to towards the coast after vertical ascent and high advection at the surface caused most of these larvae to exit the model grid at the grid boundaries. The inclusion of parameters for swimming and orientation behaviour in larvae would have greatly assisted this study.

The high self-recruitment observed within Kāneʻohe bay suggests that there is a need for regions within Kāneʻohe bay to be monitored for stressors such as pollution and over fishing to ensure that good ecosystem health is maintained and that local fish populations are able to replenish themselves. This will allow Kāneʻohe bay to continue providing important ecosystem and recreational services and continue playing significant cultural roles in the lives of the people of O'ahu, Hawai'i.

TABLES

Table 1: Release dates for each simulation. The first column is Release Date. The following columns are simulations: Advection without diffusion, PLD 55, PLD 65, PLD 75, No OVM, OVM, OVM with high density egg and OVM with low density egg.

Release Dates (month/day /year)	Advection without diffusion	PLD 55	PLD 65	PLD 75	No OVM	OVM	OVM with high density egg	OVM with low density egg
01/01/14	✓	✓	✓	✓	✓	✓	✓	✓
01/16/14	✓	✓	✓	✓	✓	✓	✓	✓
01/30/14	✓	✓	✓	✓				
02/14/14	✓	✓	✓	✓				
03/01/14	✓	✓	✓	✓	✓	✓	✓	✓
03/16/14	✓	✓	✓	✓	✓	✓	✓	✓
03/30/14	✓	✓	✓	✓				
04/15/14	✓	✓	✓	✓				
04/29/14	✓	✓	✓	✓				
05/14/14	✓	✓	✓	✓				
05/28/14	✓	✓	✓	✓				
06/13/14	✓	✓	✓	✓	✓	✓	✓	✓
06/27/14	✓	✓	✓	✓	✓	✓	✓	✓
07/12/14	✓	✓	✓	✓				
07/26/14	✓	✓	✓	✓				
12/06/14	✓	✓	✓	✓				
12/21/14	✓	✓	✓	✓				
01/05/15	✓	✓	✓	✓	✓	✓	✓	✓
01/20/15	✓	✓	✓	✓	✓	✓	✓	✓
02/03/15	✓	✓	✓	✓				
02/18/15	✓	✓	✓	✓				
03/05/15	✓	✓	✓	✓	✓	✓	✓	✓
03/20/15	✓	✓	✓	✓	✓	✓	✓	✓
04/04/15	✓	✓	✓	✓				
04/18/15	✓	✓	✓	✓				
05/03/15	✓	✓	✓	✓				
05/18/15	✓	✓	✓	✓				
06/02/15	✓	✓	✓	✓	✓	✓	✓	✓
06/16/15	✓	✓	✓	✓	✓	✓	✓	✓
07/01/15	✓	✓	✓	✓				
07/15/15	✓	✓	✓	✓				
07/31/15	✓	✓	✓	✓				

Table 2: Summary of statistical model results. Best specified statistical model selected among models representing all possible predictor combinations and their two-way interactions with release date and region of larval release denoted by ":" based on ΔAICc <= 2 and ΔBIC <= 2 (See section Statistical Analysis for more information).

Predictors *(Main effects + interactions)*	**AICc**	**ΔAICc**	**BIC**	**ΔBIC**
(To test effect of PLD) PLD + Region of egg release + Release date + PLD:Region of egg release + PLD:Release date+ Region of egg release:Release date	356697.8	0	360796.7	0
(To test effect of OVM) OVM + Region of egg release + Release date + OVM:Region of egg release + OVM:Release date + Region of egg release:Release date	105211.9	0	120438.6	0

Table 3a: Probabilities of settling by region of larval release with standard error. Probabilities are averaged over PLD and Release date.

Region	Probability	Standard Error
Inner Bay	0.912	0.001
Mid Bay	0.573	0.002
Mid Coast	0.064	0.001
Mokapu	0.003	0.026
North Bay	0.432	0.004
North Coast	4.22×10^{-5}	1.80×10^{-2}
Reef flat	0.260	0.002
South Bay	0.715	0.002
South Coast	2.30×10^{-4}	1.90×10^{-3}

Table 3b: Probabilities of settling by region of larval release with standard error. Probabilities are averaged over OVM and Release date.

Region	Probability	Standard Error
Inner Bay	0.938	0.002
Mid Bay	0.288	0.003
Mid Coast	2.28×10^{-3}	2.25×10^{-4}
Mokapu	1.54×10^{-6}	6.21×10^{-3}
North Bay	0.100	0.004
North Coast	7.10×10^{-5}	1.30×10^{-3}
Reef flat	0.062	0.002
South Bay	0.718	0.004
South Coast	4.39×10^{-10}	2.66×10^{-8}

FIGURES

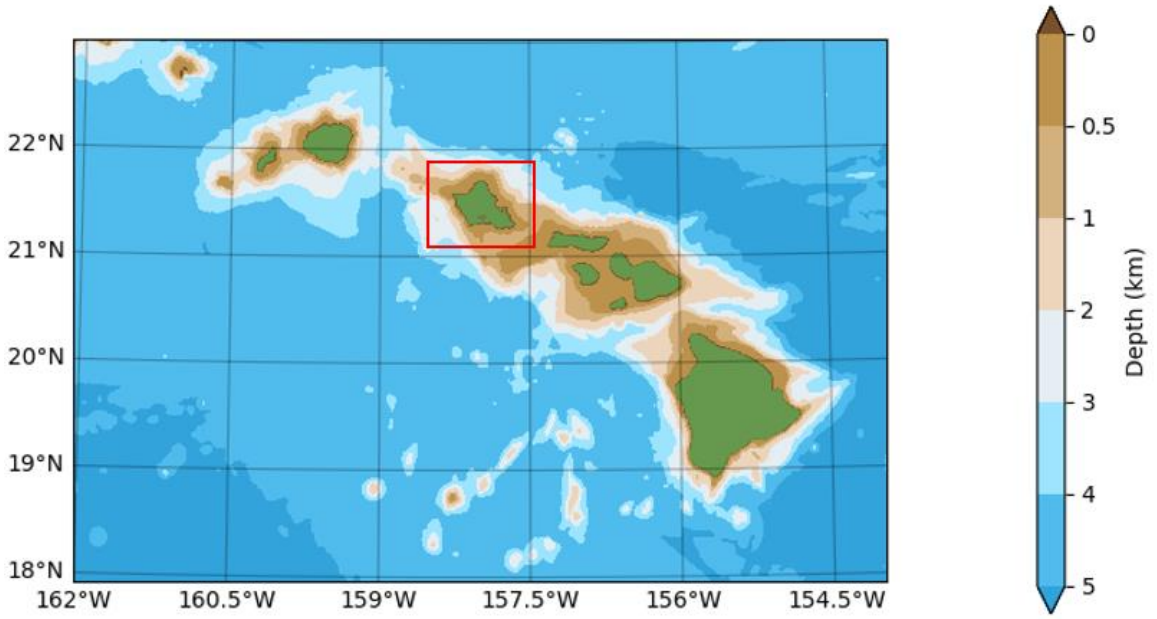
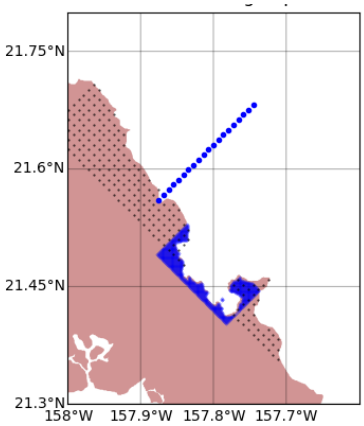


Figure 1: Study area with depth contours. Color bar represents water depth in kilometres. The island of O'ahu is outlined by the red box.

a).



b).

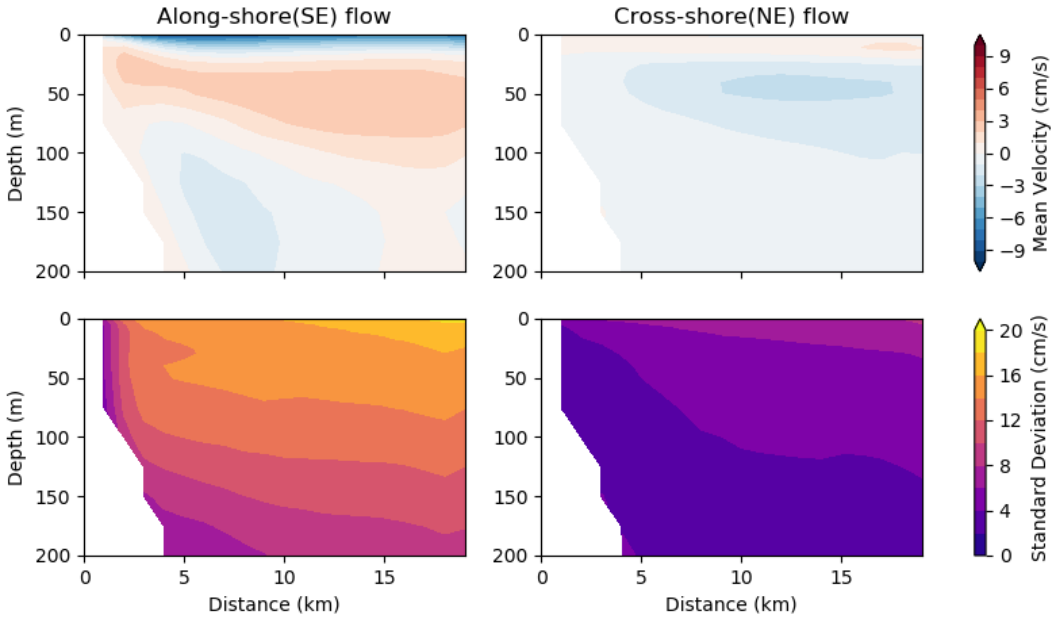


Figure 2: a). Blue dots mark a section across the windward coast of O'ahu. b). Mean velocity and standard deviation of along-shore and cross-shore currents with depth (averaged over years 2014 and 2015 from ROMS output). For along-shore, positive velocities indicate currents moving in the south-east direction and negative velocities indicate currents moving in the north-west direction. For cross-shore, positive velocities indicate currents moving away from shore in the north-east direction and negative velocities indicate currents moving towards shore (south-west direction).

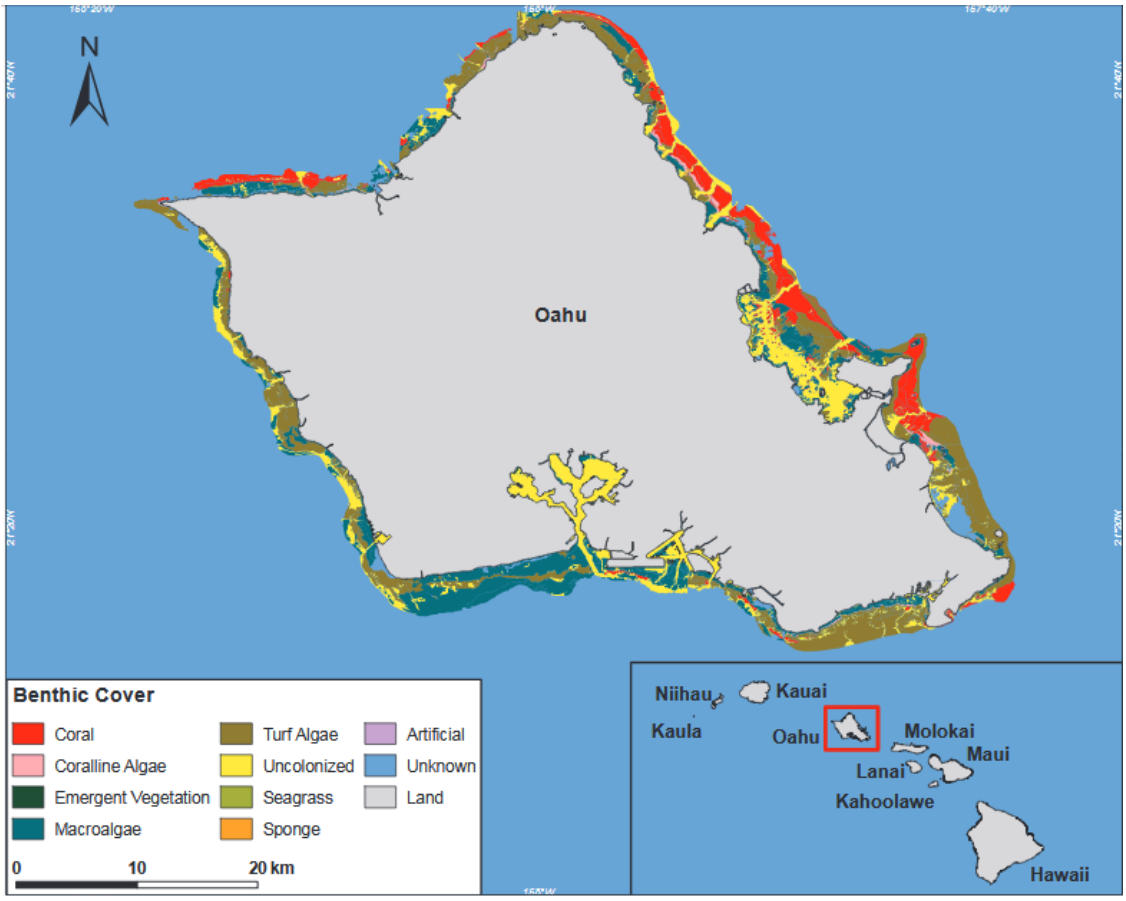


Figure 3: National Oceanic and Atmospheric Administration (NOAA), National Centers for Coastal Ocean Science (NCOOS) shallow water benthic habitat map. Fringing reef areas labelled as "Coral" on the north-eastern side of O'ahu are shaded in red. Figure from Monaco et al. (2012) with permission.

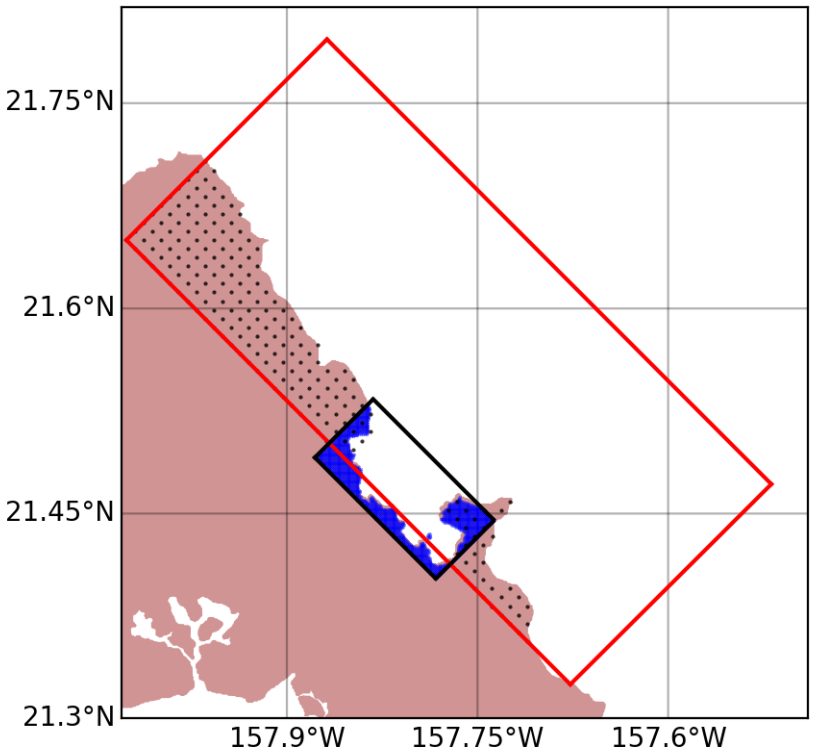


Figure 4: ROMS grids. The windward Coast of O'ahu (1 km resolution) grid is outlined in red with land areas shaded in black dots. The Kāneʻohe Bay (100 m resolution) grid is outlined in black with land areas shaded in blue.

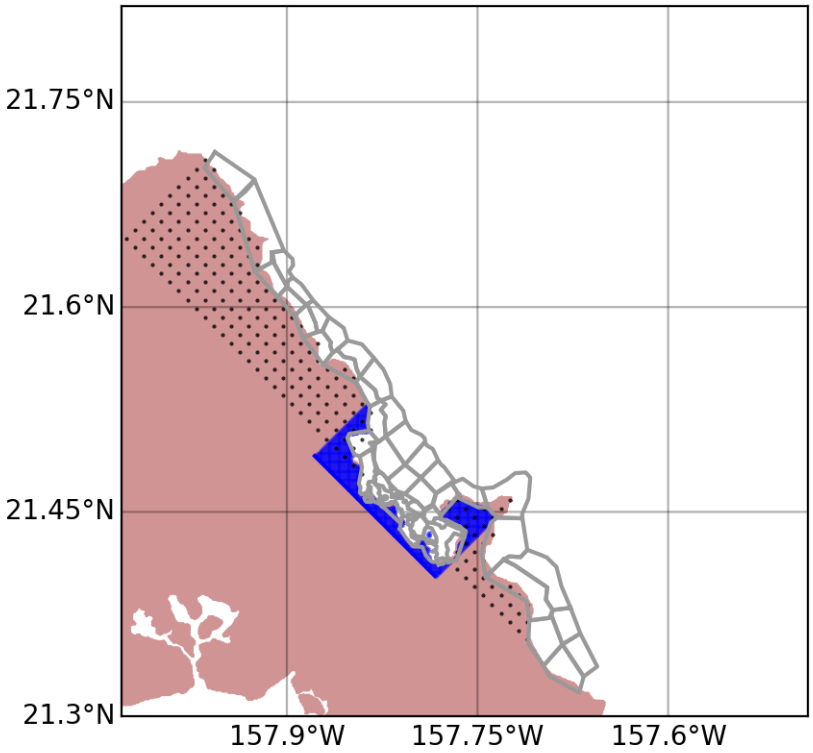


Figure 5: Fifty-three habitat polygons across the windward coast of Oʻahu outlined in grey. Pink shaded area is part of the island of O'ahu. Land areas included in the windward coast of O'ahu model grid are shaded in black dots. Land areas in the Kāneʻohe Bay grid are shaded in blue.

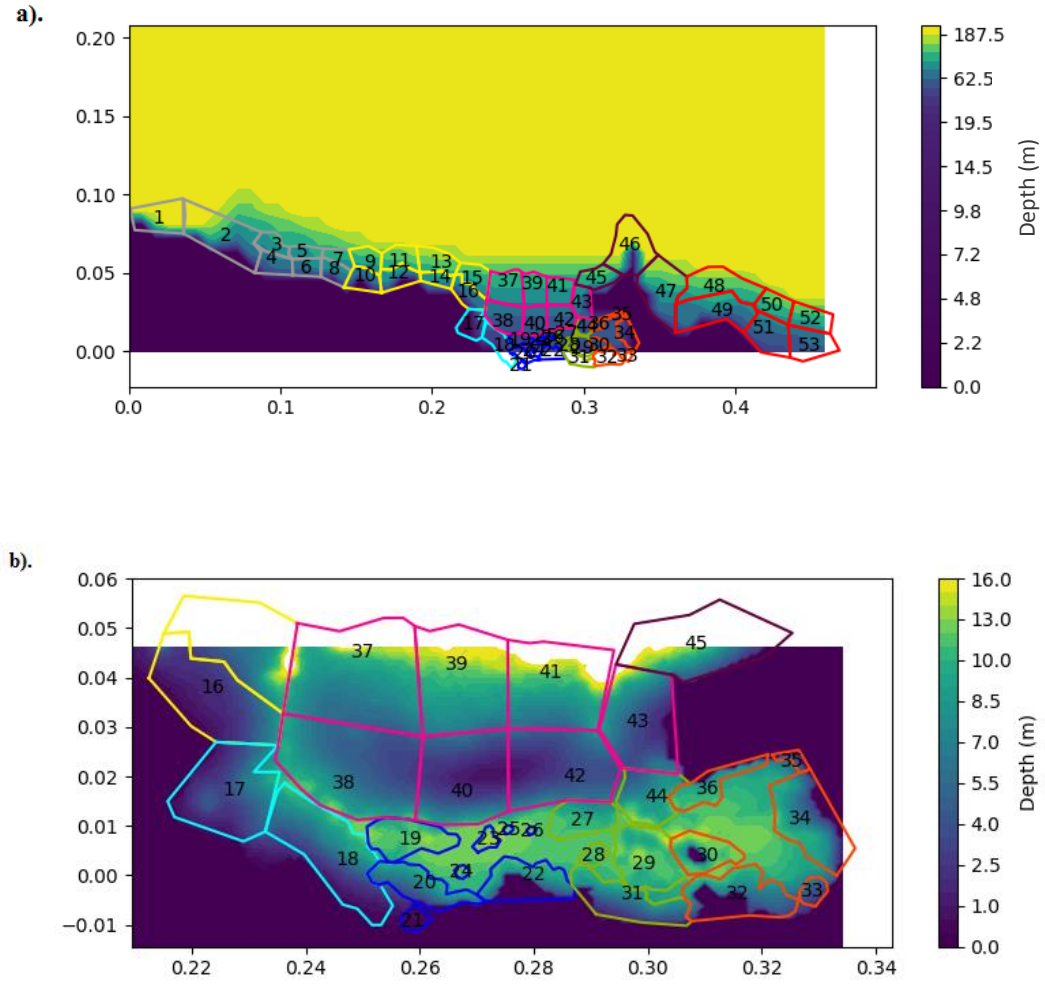


Figure 6: Numbered habitat polygons for windward coast (a) and Kāneʻohe Bay (b). The outer limit of each region varies by colour. The regions are the following: North Coast (1-8) in grey, Mid Coast (9-16) in yellow, North Bay (17-18) in light blue, Mid Bay (19-26) in dark blue, South Bay (27-29, 31, 44) in light green, Inner Bay (30, 32-36) in orange, Reef flat (37-43) in pink, Mokapu (45-47) in purple, South Coast (48-53) in red. Colour bar is depth in meters. Colour bars in a) and b) are not the same.

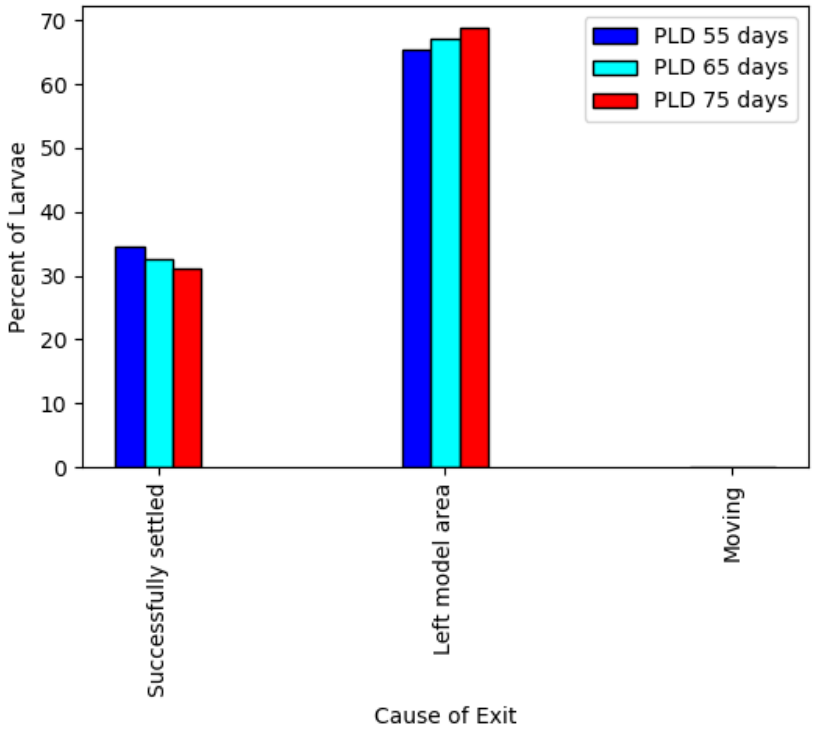


Figure 7: Cause of exit of larvae from model by the end of simulations exploring variation in PLD. Successfully settled refers to larvae that were found within the habitat polygons after the specified PLD was reached. Left model area refers to larvae that get advected off of the model grid during the simulation. Moving refers to larvae that were located within the model grid at the end of the simulation, but not in the habitat polygons.

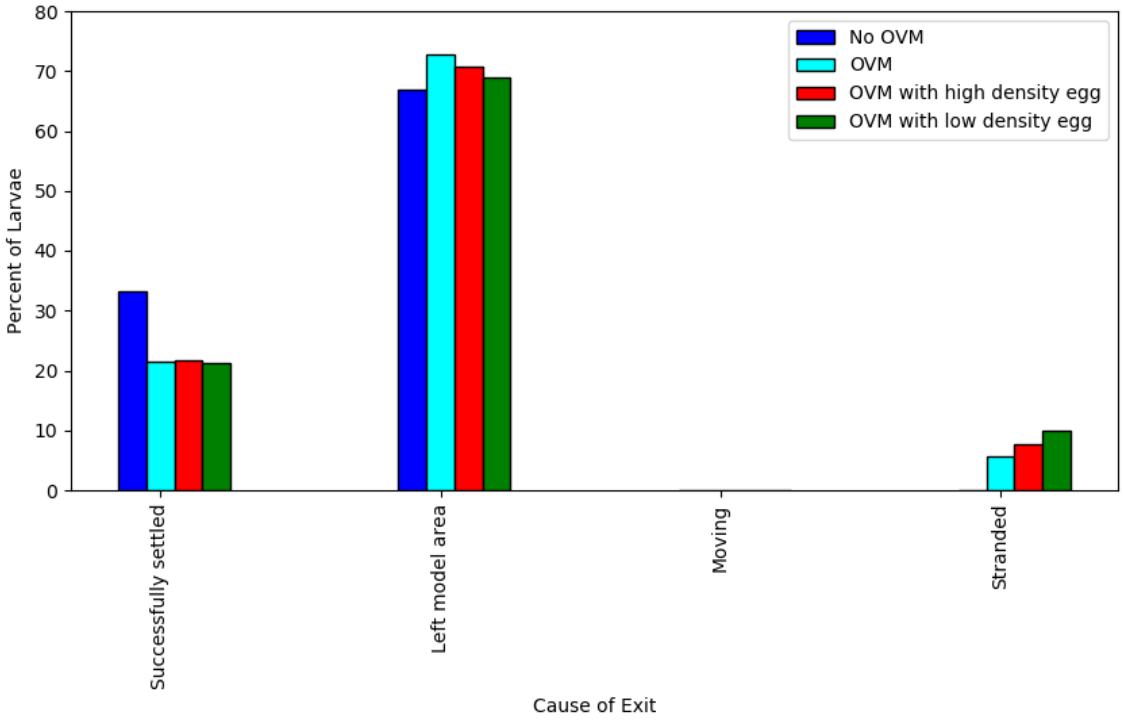


Figure 8: Cause of exit of larvae from model by the end of simulations exploring variation in OVM behaviour. OVM stands for Ontogenetic Vertical Migration. Successfully settled refers to larvae that were found within the habitat polygons after the specified PLD was reached. Left model area refers to larvae that were advected off of the model grid during the simulation. Moving refers to larvae that were located within the model grid at the end of the simulation, but not in the habitat polygons. Stranded refers to larvae that were removed from the model grid due to a model artefact.

a) b).

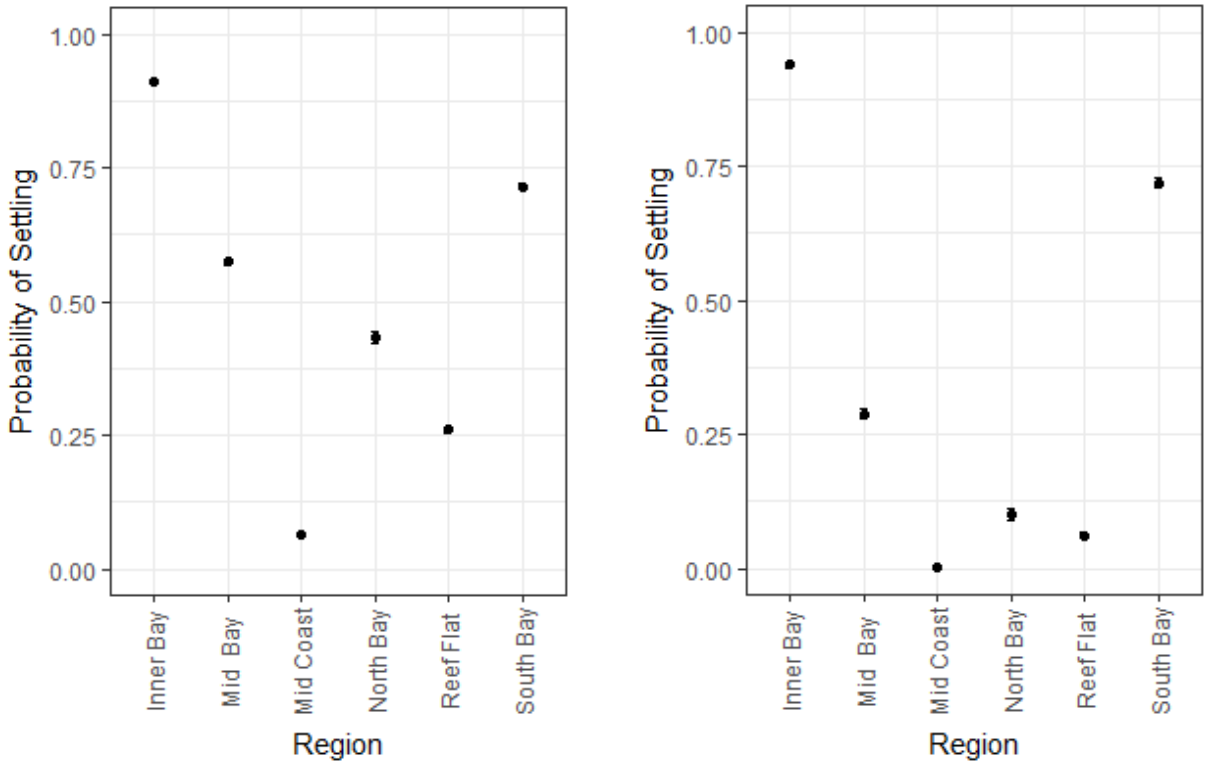
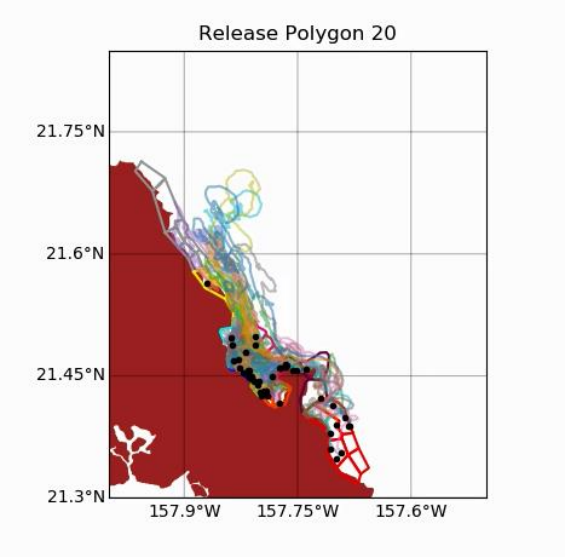


Figure 9: Predicted probability of settling by particular region of release, p.value <0.05, t-test from lsmeans package in R, confidence level used : 0.95), a). averaged over release date and PLD, b). averaged over release date and OVM.

a).



b).

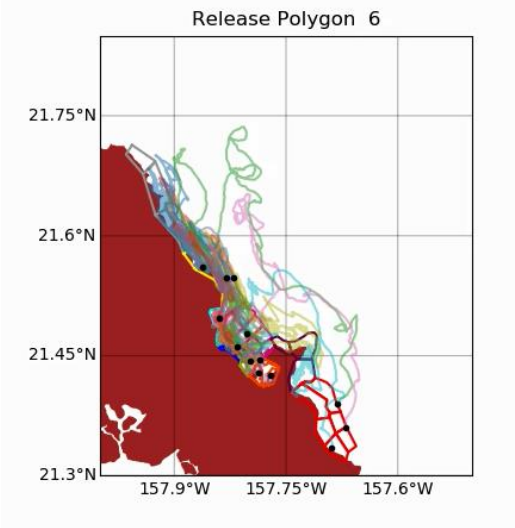
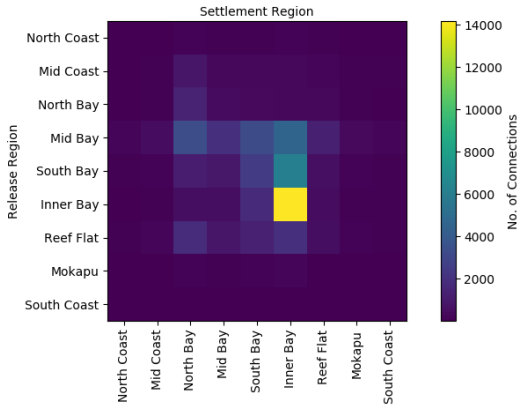
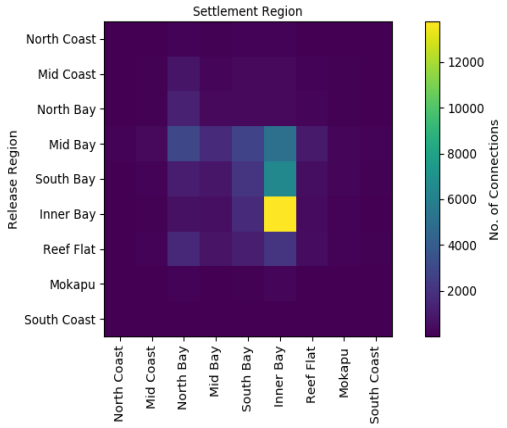


Figure 10: Most settlements occurred in Kāneʻohe bay. Black dots mark larval settlement locations. Each coloured line over the habitat polygons represents the trajectory of each larva. The high number of black dots inside Kāneʻohe bay show that most settlements occurred in Kāneʻohe bay whether larvae were released inside the bay for example in a) or outside the bay for example in b).

a).



b).



c).

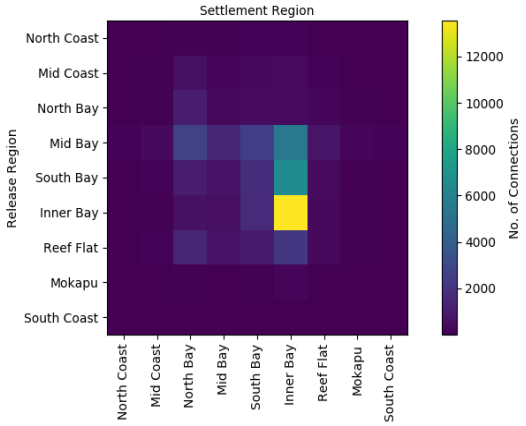
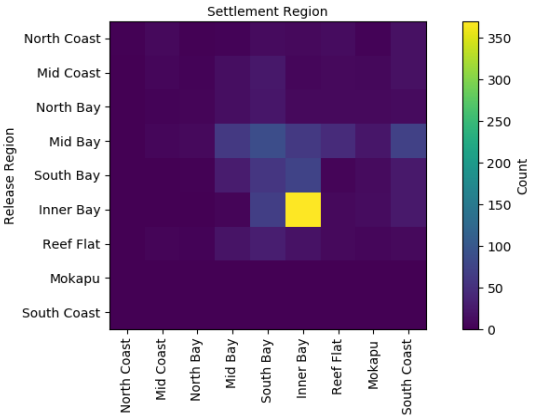
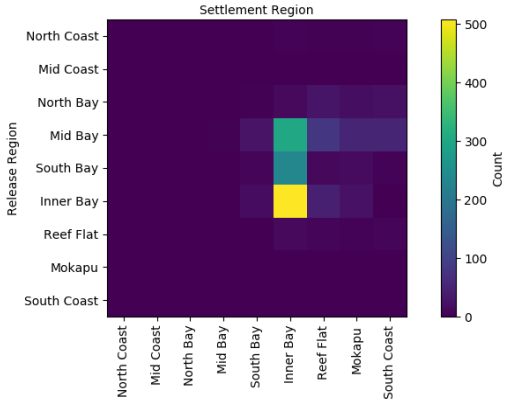


Figure 11: a). Connectivity patterns from PLD 55 days simulation, b). Connectivity patterns from PLD 65 days simulation, c). Connectivity patterns from PLD 75 days over the 32 release dates. Colour bars indicate the number of connections.

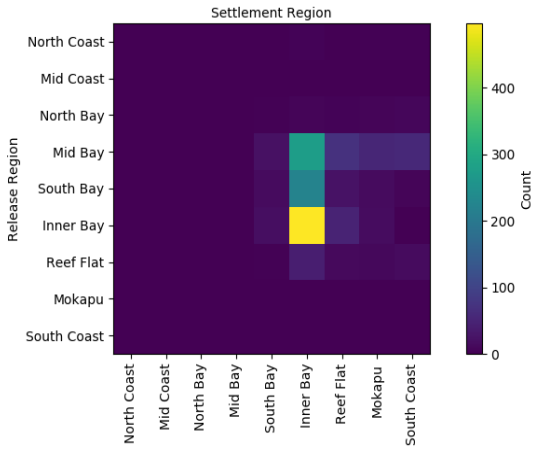
a).



b).



c).



d).

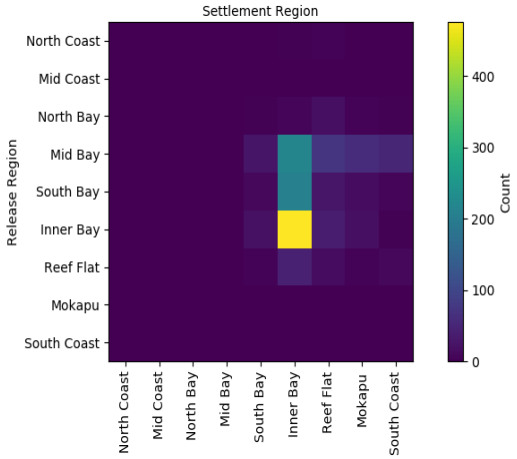


Figure 12: Connectivity patterns in simulations exploring Ontogenetic Vertical Migration (OVM) behaviour. a). Simulation with no OVM. b). Simulation with OVM. c). Simulation with OVM and high density egg. d). Simulation with OWM and low density egg. All simulations were for release date (year/month/day) 2014-01-01. Colour bars indicate the number of connections.

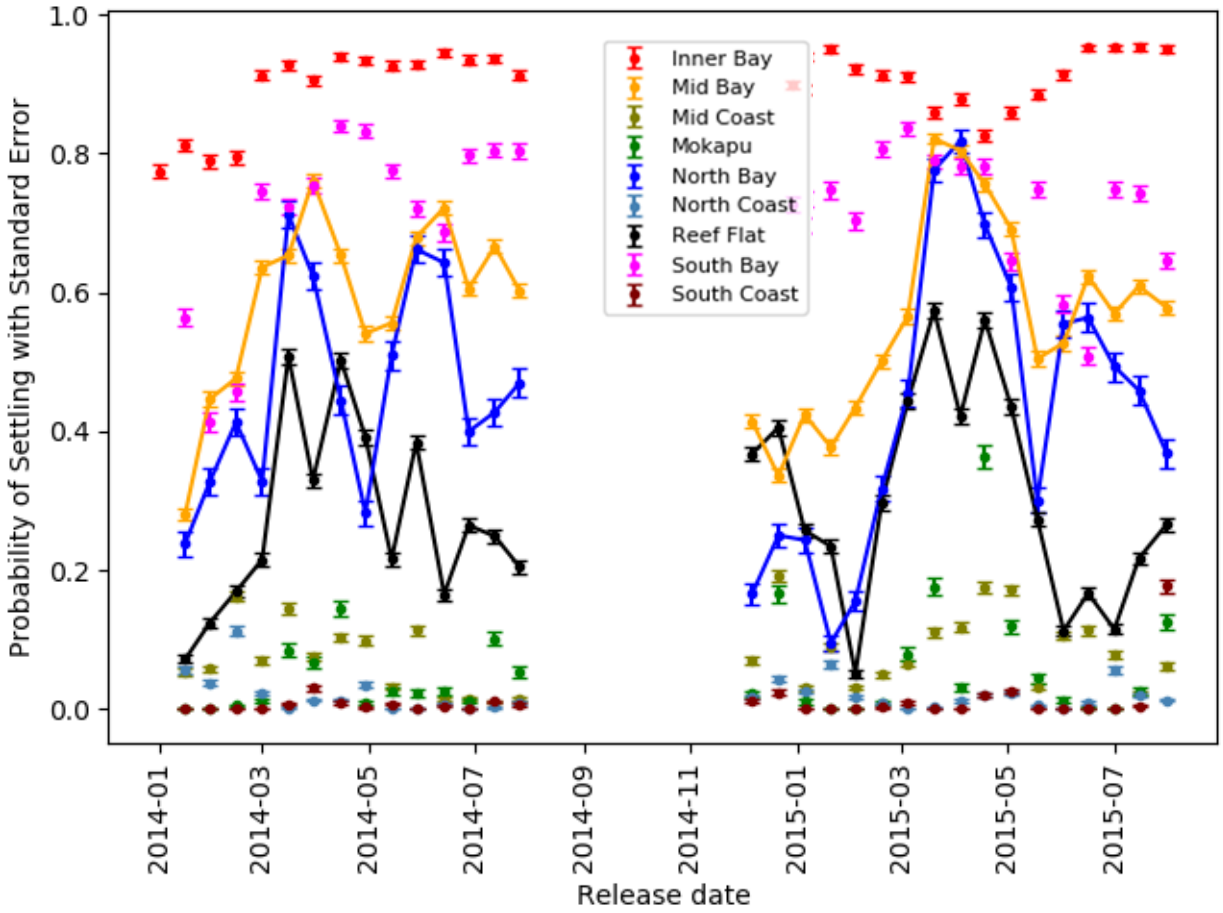


Figure 13: Predicted probabilities of settling by region of release and release date (p.value <0.05, t-test from lsmeans package in R, confidence level used: 0.95), averaged over PLD. Lines show seasonality for larvae released in Mid Bay region in orange, North Bay region in blue and Reef flat region in black.

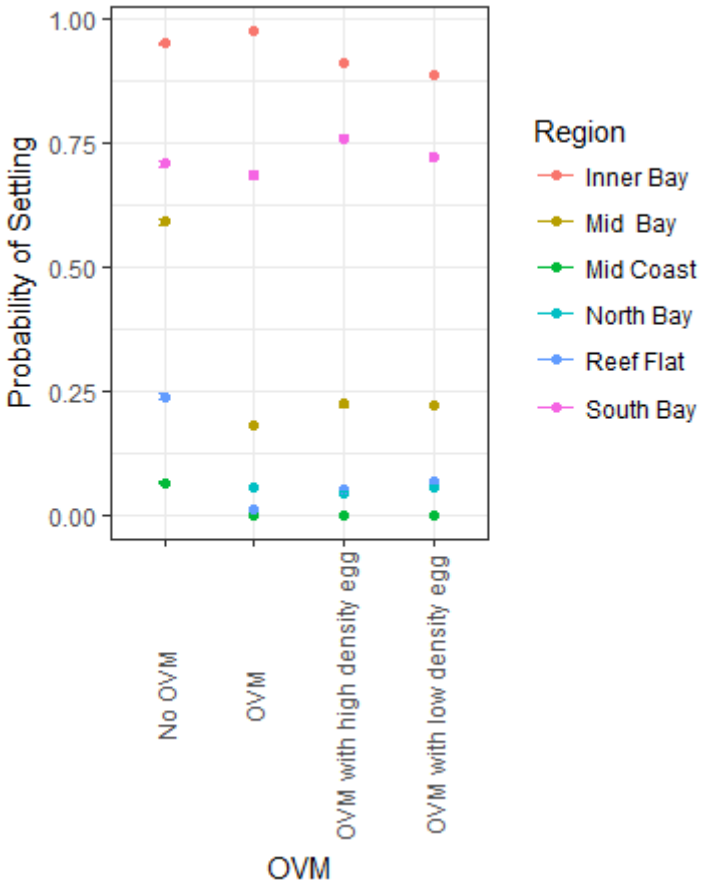


Figure 14: Predicted probability of settling by region of release and OVM (p.value <0.05, t-test from lsmeans package in R, confidence level used : 0.95), averaged over released date.

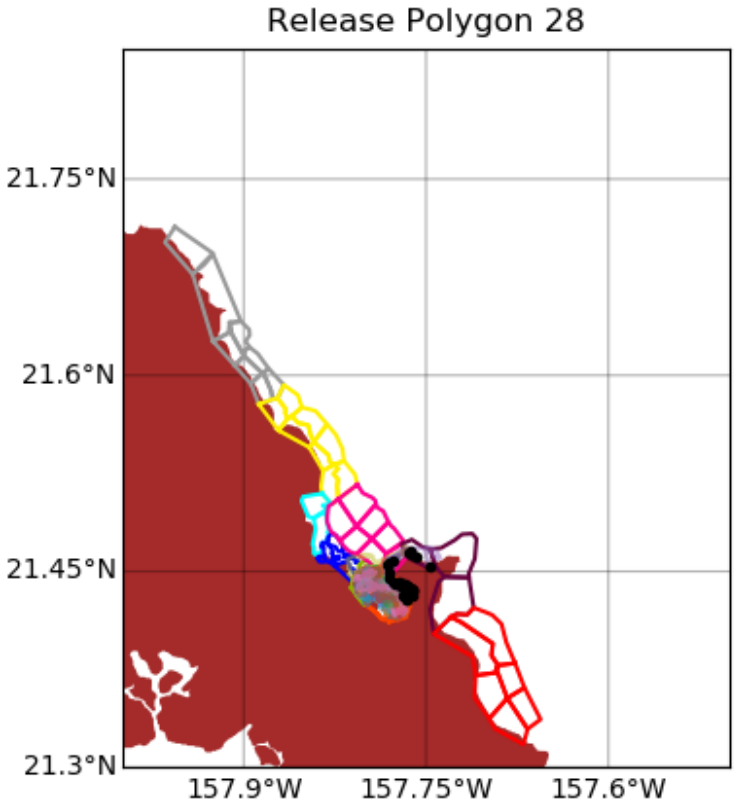
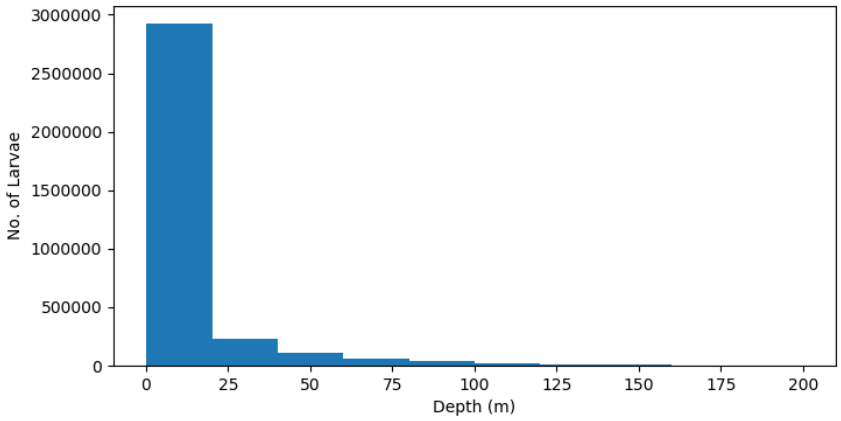
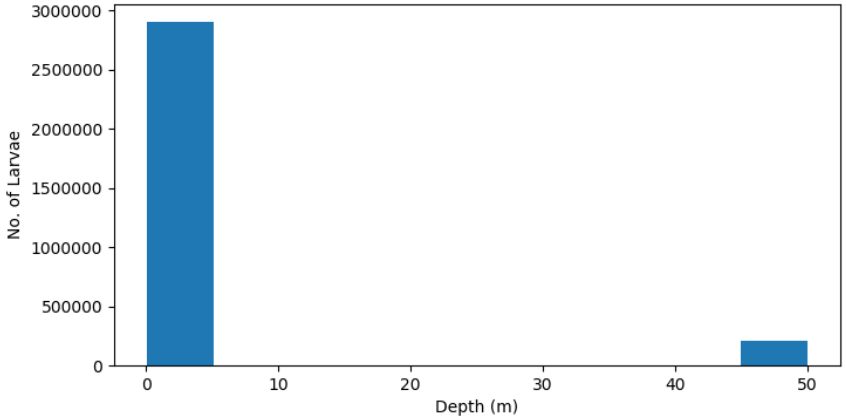


Figure 15: Trajectories of larvae released from Polygon 28 (South Bay region) during a simulation using ontogenetic vertical migration (OVM) for release date 2014-01-01 (year/month/day).

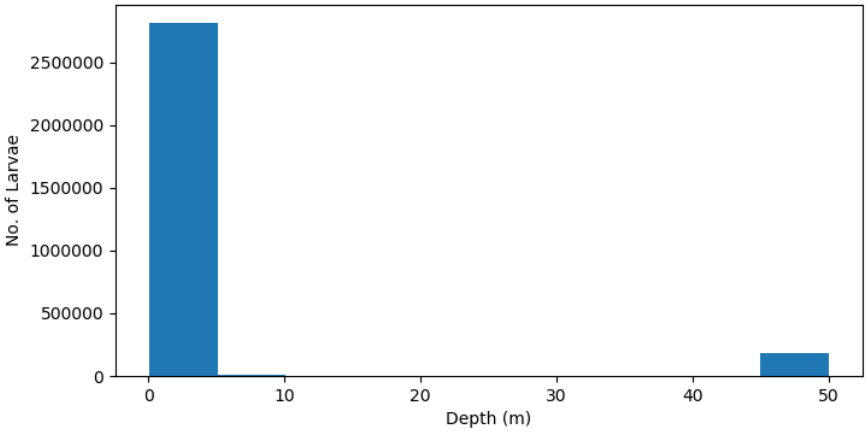
a).


3000000
2500000
2000000
1500000
1000000
500000
0
No. of Larvae
0
25
50
75
100
125
150
175
200
Depth (m)

b).


3000000
2500000
2000000
1500000
1000000
500000
0
No. of Larvae
0
10
20
30
40
50
Depth (m)

c).


2500000
2000000
1500000
1000000
500000
0
No. of Larvae
0
10
20
30
40
50
Depth (m)

d).

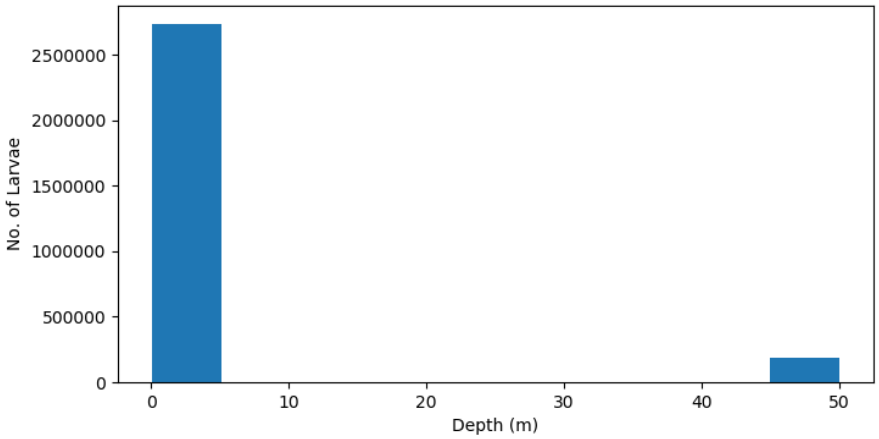
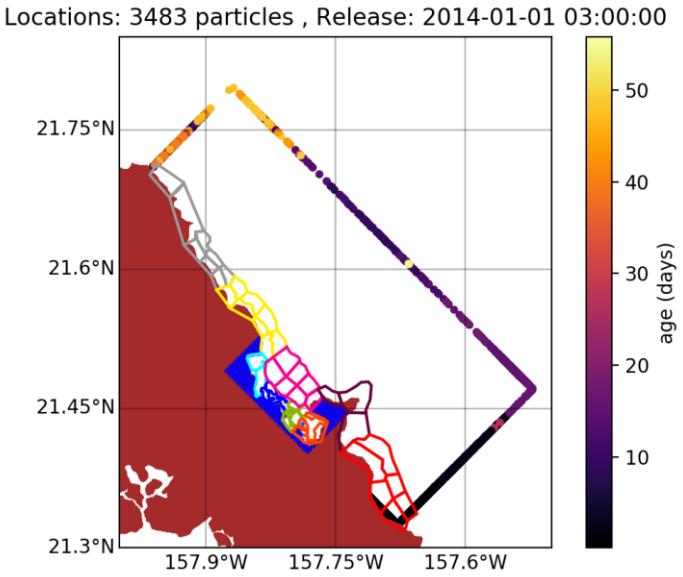


Figure 16: Depths occupied by larvae during simulations exploring ontogenetic vertical migration (OVM). a). Simulation with no OVM. b). Simulation with OVM. c). Simulation with OVM and high density egg. d). Simulation with OVM and low density egg. All simulations were for release date 2014-01-01 (year/month/day).

a).



b).

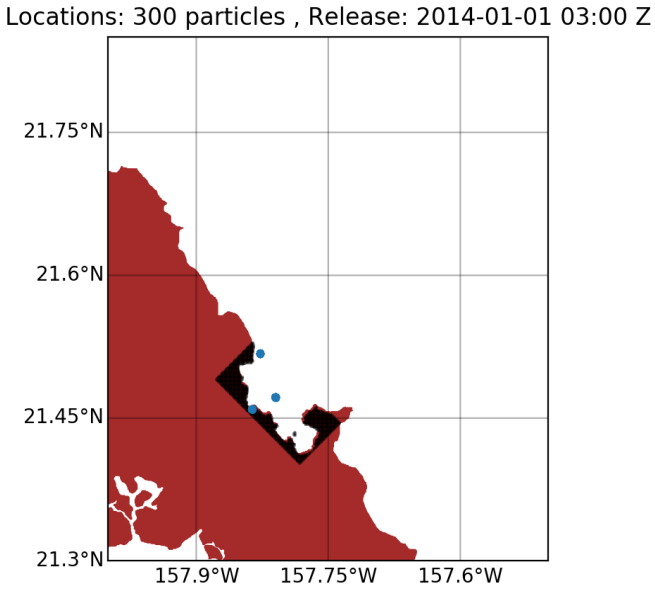


Figure 17: a). Age of larvae exiting the model at model grid boundaries in OVM simulations for release date 2014-01-01 (year/month/day). The color of the dots indicates the age of larvae in days (see color bar) at their last moment in the model grid. b). Locations were larval stranding occurred in OVM simulations for release date 2014-01-01 (year/month/day).

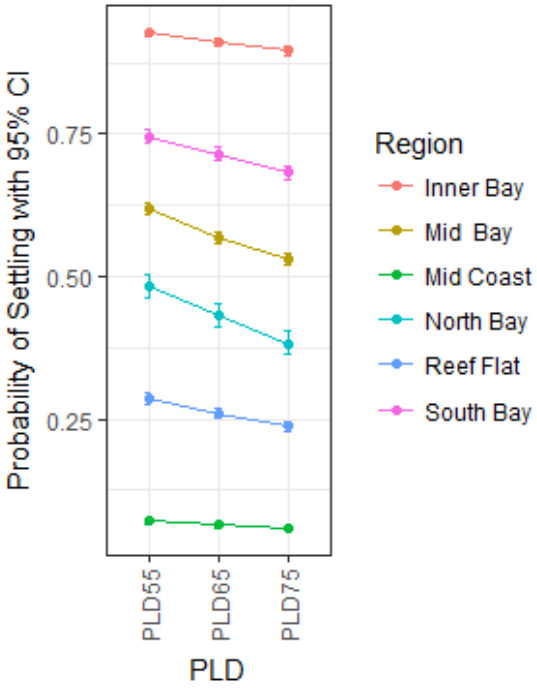


Figure 18: Predicted probability of settling by region of release and PLD (p.value <0.05, t-test from lsmeans package in R, confidence level used: 0.95), averaged over release date.

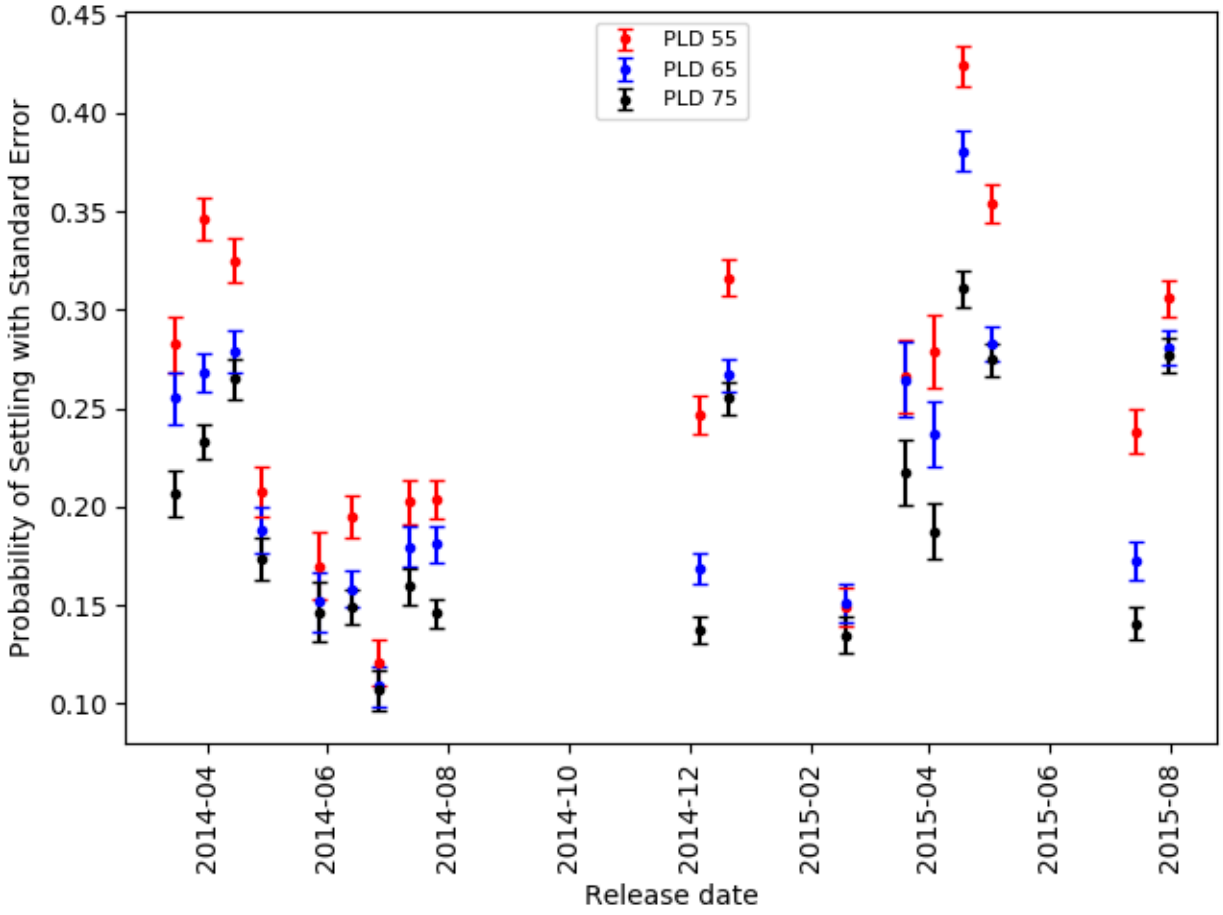
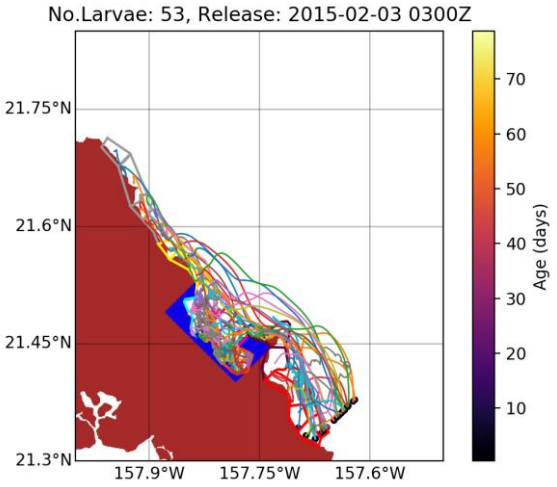


Figure 19: Predicted probability of settling by release date and PLD (p.value <0.05, t-test from lsmeans package in R, confidence level used : 0.95), averaged over region of release.

a).



b).

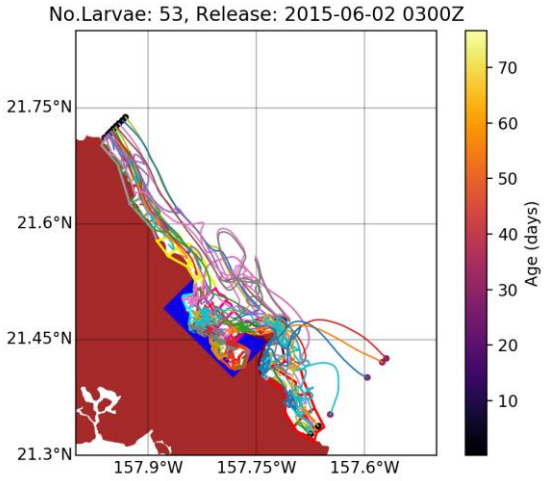
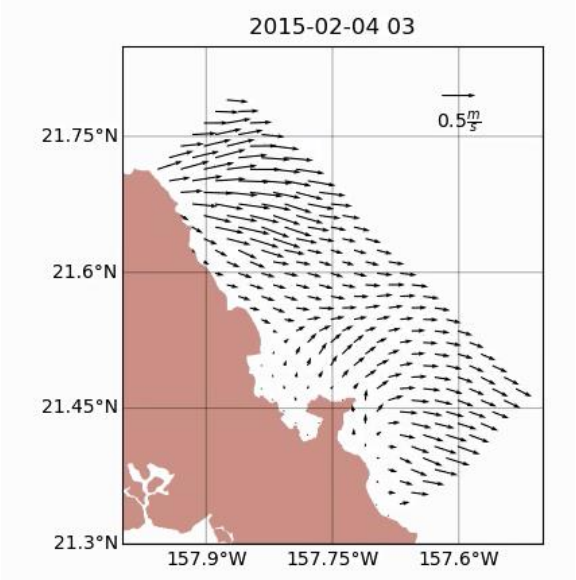


Figure 20: a). Larvae moving in alongshore direction (South-east ward). b). Larvae moving in alongshore direction (North-west ward). Release dates are written in (year/month/day) format. Each coloured line is the trajectory of each larva. The coloured dots signify the last position of the larvae in the model grid. The colour of the dots indicates the age of larvae in days (see color bar) at their last moment in the model grid.

a).



b).

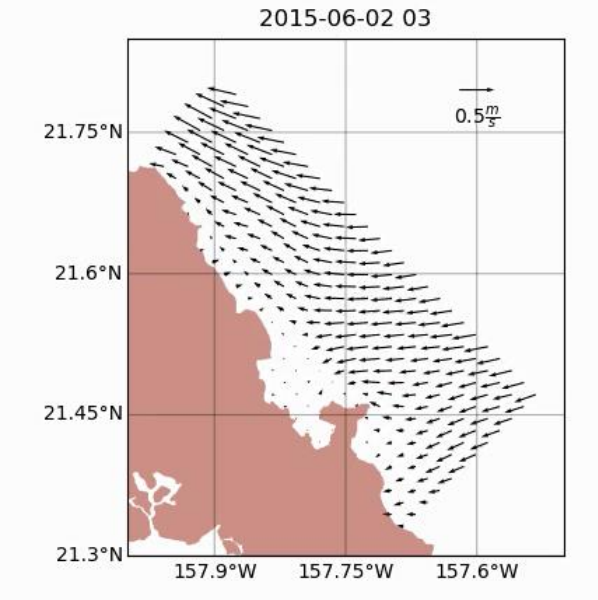
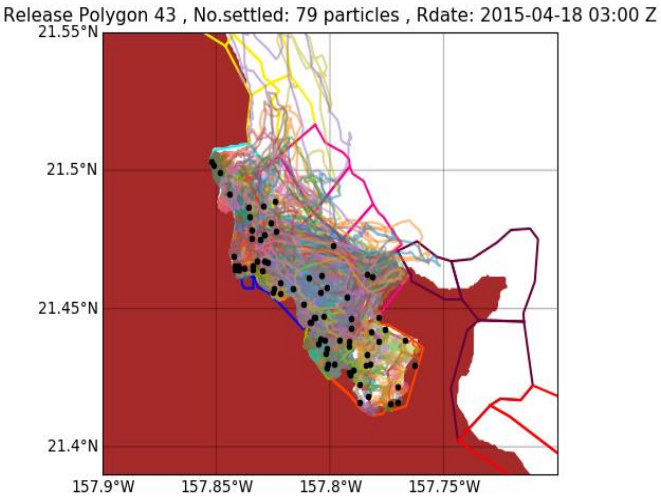


Figure 21: Current patterns at 3 m depth in windward O'ahu on a). 2015-02-04 at 3 am UTC and b). 2015-06-02 at 3 am UTC.

a).



b).

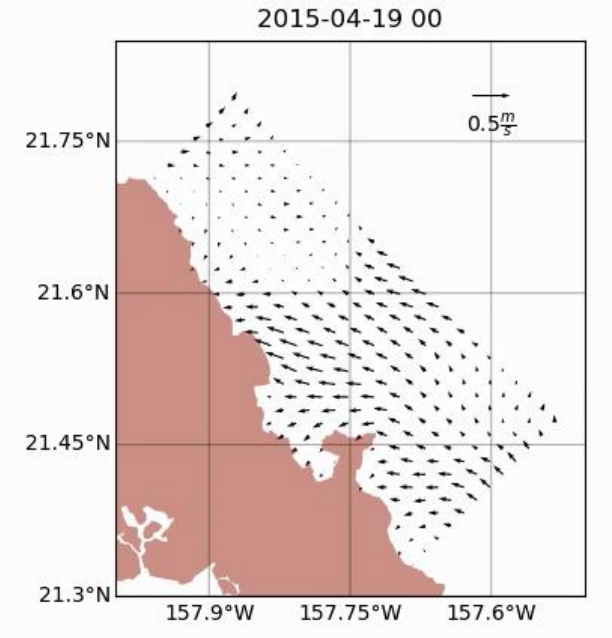
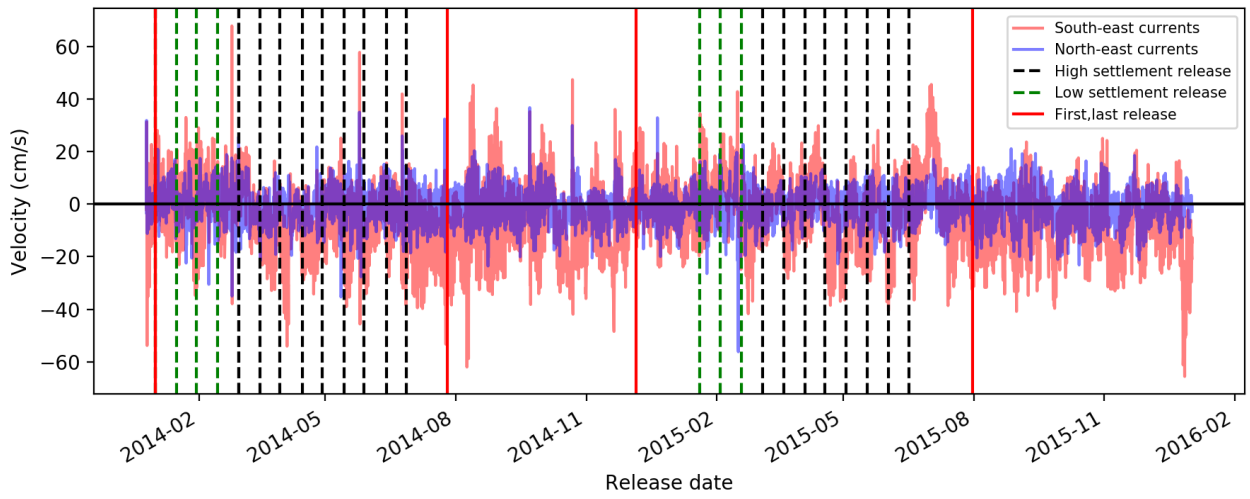


Figure 22: a). Trajectories of larvae released in polygon 43 (Reef flat region) in April 2015 that successfully settled in the model. b). Onshore currents with in one day after April 2015 release.

a).



b).

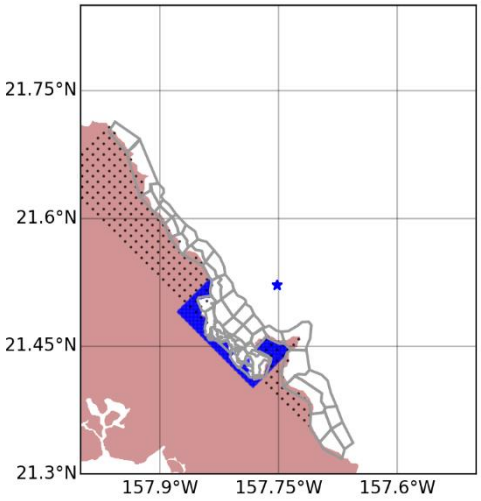


Figure 23: a). Time series of along shore flow (South-east currents) and cross shore flow (North-east currents) over 2014 and 2015 at 3m depth at a point in front of Kāneʻohe Bay. Red vertical lines mark the first and last release dates for the 2014 and 2015 spawning seasons. Green vertical dashed lines mark the release dates with low settlement success and black vertical dashed lines mark the release dates with high settlement success. b). The point where the time series was obtained from is marked with the blue star.

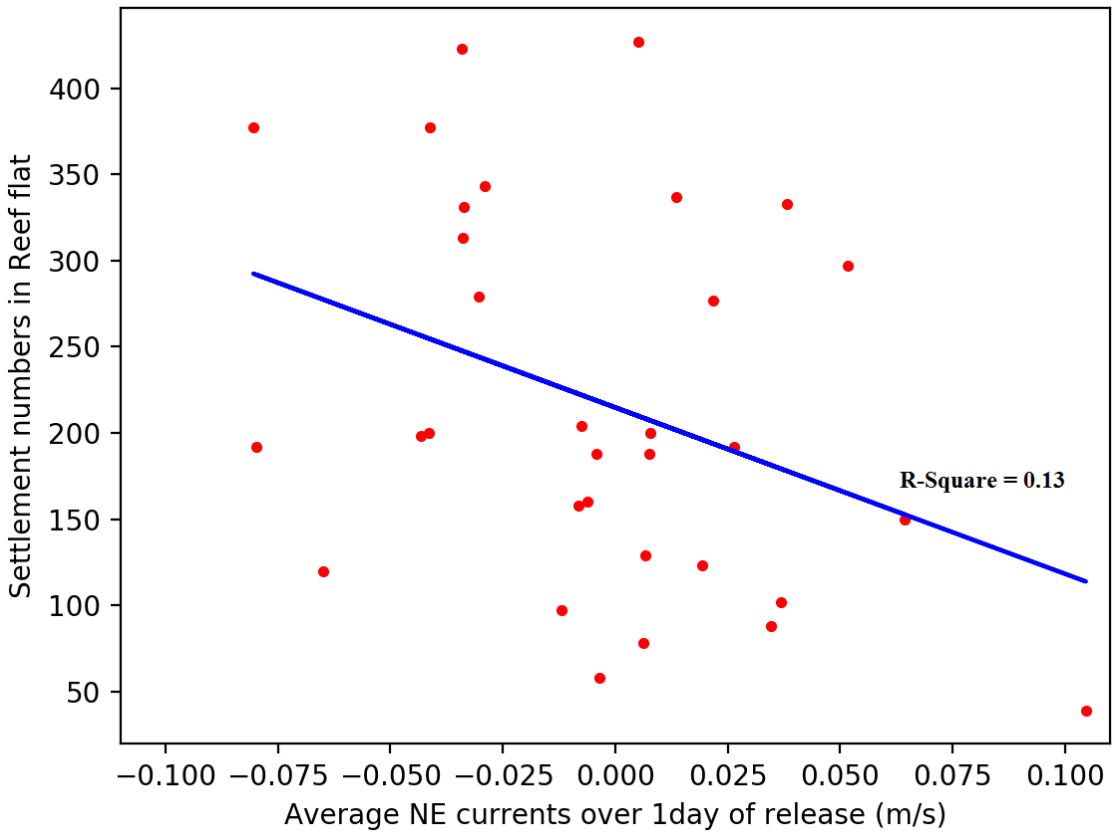
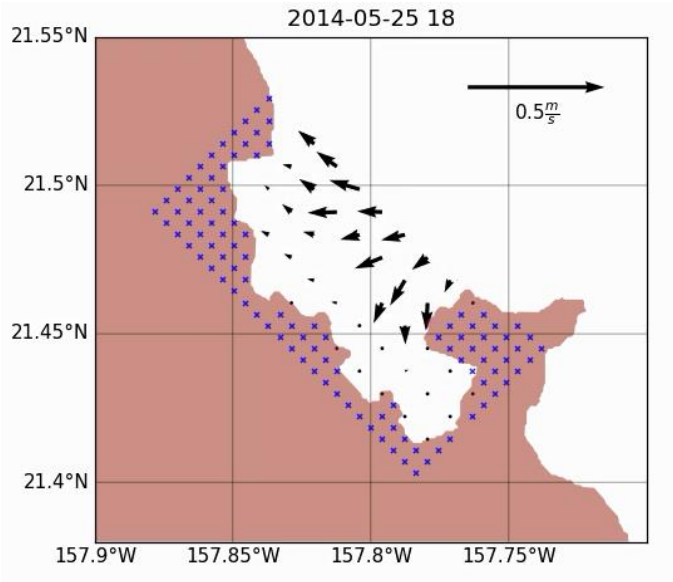


Figure 24: Average cross shore currents over a day of release against settlement numbers for larvae released in the Reef flat region. The currents were obtained from the point shown in Figure 23 b.

a).



b).

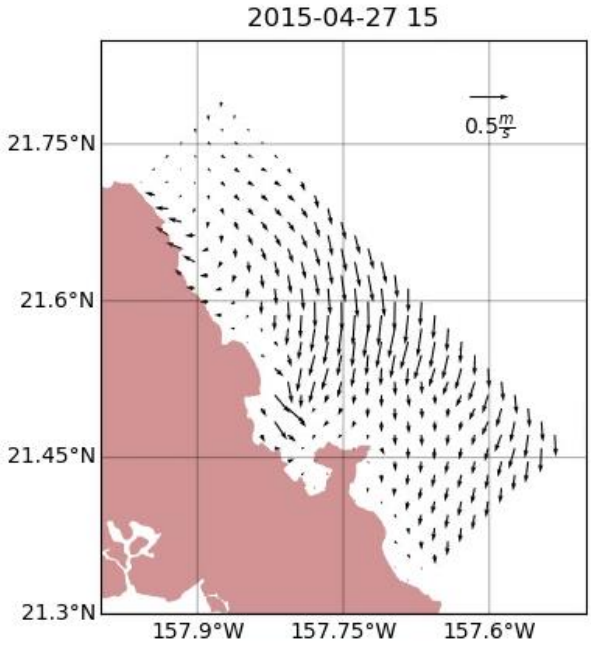


Figure 25: a). Current patterns at 3 m depth in Kāneʻohe Bay on 2014-05-25 at 6 pm UTC showing current flow into the Inner Bay region during flood tides. b) Onshore currents and current flow from the northern parts of Kāneʻohe Bay to the southern and inner parts of the bay.

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